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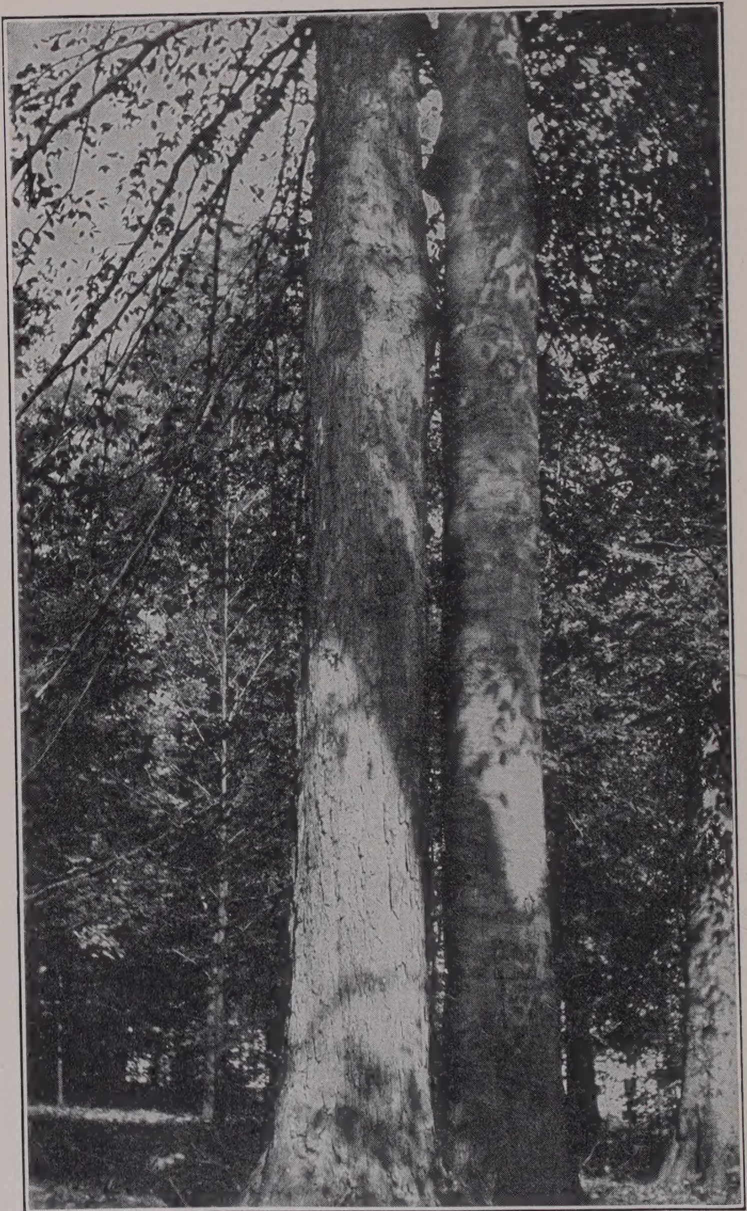
A College Textbook of Botany
for
First Year Students



Beech-Maple Climax, Campus, Indiana University. Photograph by Glenn W. Blaydes.

FRONTISPIECE

A College Textbook of Botany for First Year Students

BY

DAVID MYERS MOTTIER
PROFESSOR OF BOTANY AND HEAD OF THE DEPARTMENT
IN INDIANA UNIVERSITY

WITH THREE HUNDRED THIRTY-THREE ILLUSTRATIONS

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PREFACE

This book has been prepared for use in the introductory or first year's course in botany in the university or for an equivalent course in a junior college.

There is no question in the author's mind that the fundamentals of this subject should be the same in all colleges whether the aim of the college training be that of the application of knowledge to some vocation or for the advancement of knowledge for its own sake.

After many years of experience in teaching elementary botany in the university, the author is convinced that the beginner who has any taste for the subject or in whom a desire to know something of plant life may be stimulated, has first of all an interest in a knowledge of plants as living individuals as manifested in their form, structure, function, reproduction and in their adjustment to the places in which they live.

The method of instruction in Indiana University includes individual laboratory work and lectures supplemented by the text book, outside reading and the quiz. The laboratory work is centered upon materials with which the student has direct personal contact. The lectures deal with a broader presentation and generalizations upon such topics as evolution and heredity. This text is not the author's lectures done into book form. A text book is to be read over and over, while a lecture is to be heard but once.

The author has endeavored to present the subject matter in concrete form, including if possible the material used in observation, or in the specific type for life-history study. The student usually associates his knowledge of

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structure, function, and life-history with some definite plant or some part of a plant.

A number of good text books have been placed in the hands of students within the past thirty-five years by the author, and the most common complaint has been to the effect that the book in question had a little to say about too many plants with which the student was not acquainted and not enough about any one plant to enable him to connect his knowledge acquired in the laboratory with the data presented in the text-book.

In the preparation and arrangement of materials, the author has been guided largely by pedagogical principles acquired through long experience and not by the desire to make an elementary scientific treatise. The book is not intended to take the place of such classical texts as those of Strasburger, Campbell, Coulter, Barnes and Cowles, etc. Whenever feasible, the human interest side of the subject has been referred to or briefly discussed.

Most of the illustrations are original, having been prepared by the author or for him by one of his colleagues. Illustrations from other authors have been used but in nearly all such cases the figures borrowed have been either redrawn or photographed. Some have been modified in redrawing. In every case due credit is given in the legend pertaining to the figure.

The author desires to acknowledge his obligation to all those who have given aid or council in any way, and to all authors from whose works illustrations have been borrowed. He wishes to express his indebtedness especially to the following authors and their publishers: Douglas Houghton Campbell (Mosses and Ferns, and University Text-Book of Botany, Macmillan & Co.); Frederick Orpen Bower (Botany of the Living Plant, Macmillan & Co.); William Chase Stevens (Plant Anatomy, P. Blakiston's Son & Co.); Charles J. Chamberlain (Coulter and Chamberlain, Morphology of

Gymnosperms, University of Chicago Press); Bradley Moore Davis (Bergen and Davis, Principles of Botany, Ginn & Co.); Otis W. Caldwell, (Bergen and Caldwell, Practical Botany, Ginn & Co.); C. Stuart Gager, (General Botany, General Botany, P. Blakiston's Son & Co.).

To his colleagues in the department of botany in Indiana University, he desires to record his appreciation of the benefit derived from suggestions and helpful criticisms offered from time to time.

DAVID M. MOTTIER.

INDIANA UNIVERSITY
1929

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INTRODUCTION

THE BIOLOGICAL SCIENCES

All living organisms known to science may be placed in either one or the other of two great sub-divisions, or kingdoms, namely, plants and animals.

All those sciences dealing with plants and plant life as it now exists constitute the subject of Botany, and those pertaining to animals, the subject of Zoölogy. Each of these two great subjects comprises many subdivisions, some of which, like Bacteriology, Human Physiology, and the more recently segregated subject, Genetics, are often regarded as separate sciences. All the sciences dealing with living organisms constitute, therefore, the subject of Biology. The biological sciences now generally recognized as such are: Botany, Bacteriology, Human Physiology, Zoölogy, and Genetics. The subject of Genetics as applied to plant life pertains to the experimental study of heredity.

THE PLANT KINGDOM

For convenience of study and presentation, plants are grouped into great subdivisions. Trees, bushes, crop plants, garden plants, etc., all bear seeds and *spores*. They are called seed-bearing plants, *Spermatophyta*. Those familiarly recognized as ferns, fern-like plants, horse-tails, or scouring rushes, and club mosses constitute the *Pteridophyta*. Mosses and liverworts represent the *Bryophyta*. Moulds, mildews, mushrooms, rusts, smuts, and the like, make up the *Fungi*. Green, or blue-green threads and films, and sea weeds are the *Algae*. Plants familiarly known as *Lichens* represent, with few exceptions, a combination of an alga and a fungus. Certain microscopic plants, appearing individually colorless, and popularly known as "germs" or "microbes" are the *Bacteria*. There is also a group of low organisms, revealing very distinct animal as well as plant characteristics, known as the *Slime Moulds*.

Algae, fungi, and bacteria constitute the *Thallophyta*. Thallophyta, Brophyta, and all living Pteridophyta, bear *spores* only.

All of these groups of plants differ greatly from one another in appearance, structure, and life habits; but all have one thing in common: they are composed of cells, which represent the units of structure and function. Every plant or animal known to science consists of either one cell or two or more cells held together. Individuals consisting of one cell are known as unicellular plants; those of more than one cell, multicellular plants. Cell colonies are aggregates of similar cells definitely or indefinitely placed together.

An Individual Plant.—Each individual, however large or small, is capable of carrying on all the life processes necessary for the maintenance of its existence throughout a certain period of time and for the reproduction of its kind. These life processes are of two kinds, vegetative and reproductive.

As an illustration we shall select a young plant which grew from a seed as shown diagramatically in Fig. 1. The body of such a plant consists primarily of an axis, the lower end of which growing downwards into the soil is the root (*r*), whereas the upper end growing upwards above the ground is the shoot, or stem (*s*).

Some Differences between Stem and Root.—The stem bears leaves, flowers, and fruits; it is made up of nodes and internodes. That part of the stem from which a leaf or leaves arise is a node; the space between any two successive nodes is an internode. The stem ends in a

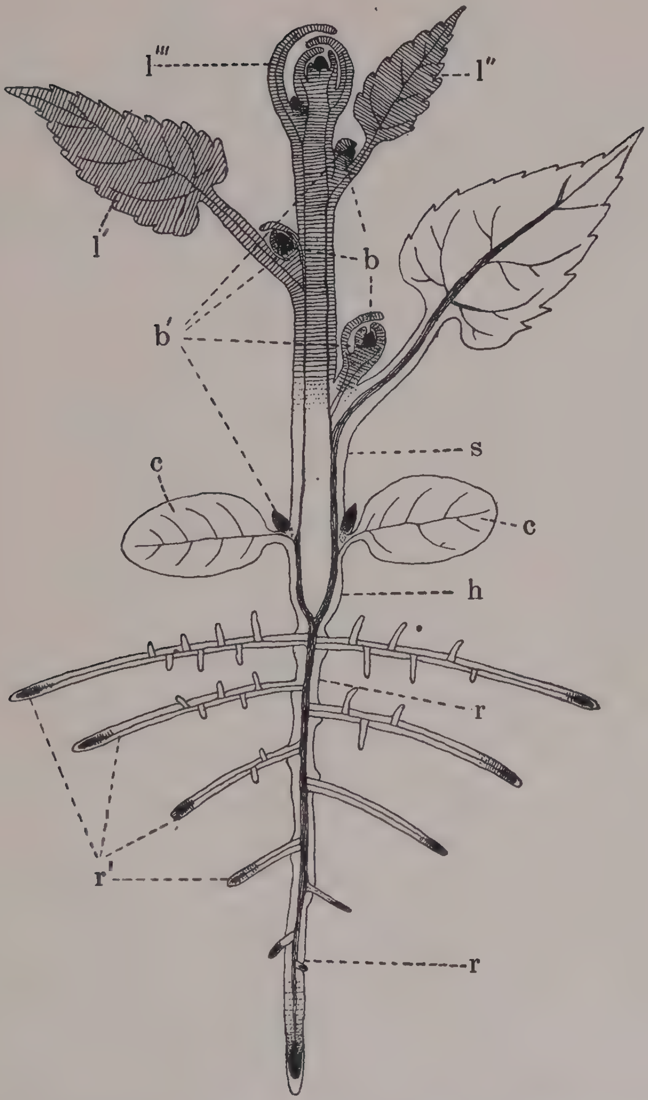

FIG. 1.—Diagram of a dicotyledonous plant. *r*, primary root; *r'*, secondary roots; *s*, shoot, stem; *h*, hypocotyl, that part of the stem between cotyledons and root; *c*, *c*, cotyledons; 1–1''', leaves; *b*, buds; Parts in black are growing points, those shaded with parallel lines are elongating or enlarging. (Adapted from Sachs.)

bud. A bud is the growing point of a stem usually covered wholly or in part by some kind of leaves. These leaves may be scale leaves, young foliage leaves or both, or floral leaves. The growing end of the stem is composed entirely of embryonic tissue or *primordial meristem.*

Ordinarily the branches of the stem arise in the axils of the leaves. When large enough to be recognized with the unaided eye they appear as buds (*b*). These are called axillary buds to distinguish them from the terminal bud of the primary stem. Buds may arise also from other parts of the plant as will be pointed out in a later paragraph. Stem branches arise from the surface of the main branch or parent branch.

Roots are cylindrical organs which as a rule are similar in plants whose stems differ very greatly in form and structure. They do not bear leaves. The growing point is covered by a *root cap.* The growing point of the root is also composed of primary meristem. Secondary or branch roots (r') arise from more centrally located tissue of the parent root. The younger parts of roots a short distance back of the growing point bear root hairs, structures which increase the absorbing surface of the root. The internal structure of roots and stems differs very much in detail.

Functions of Stem, Leaf, and Root.—Primarily the stem maintains the form of the plant above the ground, supports the leaves, flowers, and fruits, and transports water with dissolved mineral salts received from the roots to its various members. The stem transports also digested foods from places in which they are produced to places where they are needed in growth or stored for future use. The green parts of stems make food also.

Foliage leaves manufacture carbohydrates, from carbon dioxide and water, synthesize certain nitrogenous foods, and evaporate water.

The work of roots consists in anchorage and in the absorption of water and solutes. Food is stored to some extent in ordinary roots.

Throughout the range of plants there are many modifications in the form, structure, and special functions of roots, stems and leaves. These modifications are usually correlated with some special function and adaptation to the environment.

TEXT BOOK OF BOTANY

CHAPTER I

THE PLANT CELL

General Description.—A general idea of a typical plant cell may be obtained by direct observation of a leaf of the small, seed-bearing aquatic plant, Elodea, or of the moss, Funaria, or some other suitable plant.

Viewed from the surface with the microscope, the cells of the leaf of Elodea, except at the margins, appear generally rectangular in outline, as shown in Figure 1. At the first glance, the most conspicuous thing seen is the green color, due to numerous rounded green bodies, the *chloroplasts*, which may be somewhat evenly distributed in the cell, or aggregated in masses (Fig. 2, *ch*). Each cell has a thin, colorless wall. With the exception of the midrib, the leaf is only one cell in thickness, and it must be remembered that each cell appearing four-sided in outline, is not flat like a sheet of paper, but in the form of a box with six sides.

Lining the entire interior surface of each cell is a very thin, colorless layer of living substance, the cytoplasm (*cy*), in which are held or embedded the conspicuous chloroplasts (*ch*). At some point in this cytoplasmic layer is a more refractive, or greyish, rounded body, the *nucleus* (*n*). In the live cell the nucleus is not conspicuous, and may not be readily observed.

In the central part of the cell is a large cavity, constituting the larger part of the volume of the cell, the *vacuole* (*v*), which is filled with a watery fluid, the *cell* *sap*. In some cells strands of cytoplasm traverse the vacuole, and upon them chloroplasts may be located.

In certain cells a striking feature is the movement of the chloroplasts, which may be seen to pass down one side of the cell, across the end, and return along the opposite side and end, thus making a complete rotation. The movement of the chloroplasts is due to the motion of the innermost layer of cytoplasm, i.e., that next to the vacuole, the chloroplasts being carried along with the moving cytoplasm. Visible cytoplasmic movement is a conspicuous phenomenon in many adult cells. In certain cells, as those of the stamen hairs of the spiderwort, Tradescantia, the movement takes place in different directions in different parts of the same cell, thus constituting a sort of circulatory, instead of a rotary movement.

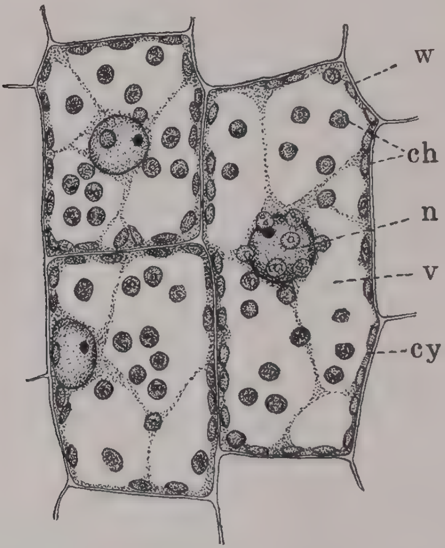

FIG. 2.—Cells from the leaf of Elodea. *w*, cell wall; *n*, nucleus; *ch*, chloroplasts; *v*, vacuole; *cy*, cytoplasm.

It should be borne in mind that it is not the entire cytoplasmic layer that is in visible motion, but merely the inner, and more fluid, part next to the vacuole. The cytoplasm lying nearest the cell wall, and in contact with it, is stationary. The exceedingly thin surface layer next to the cell wall, which constitutes the outer surface of the cytoplasm, is the *plasma membrane.* The plasma membrane is exceedingly thin, colorless, homogeneous, and of a much firmer consistency than the rest of the cytoplasm. It is now regarded as the more sensitive part of the cell, i.e., it is the part which responds to stimuli, and which tends to regulate the permeability of the cell to various substances.

From the foregoing we may now define a cell as a nucleated mass of cytoplasm having a common and continuous plasma membrane. A cell may contain two or more nuclei, in which case it is a multinucleated cell. A multinucleated cell is often called a *coenocyte.*

We shall now consider cells from the tip of some growing organ such as a root or stem, which has been properly killed (fixed), sectioned and stained, in order to learn more in detail of their internal structure. In a young cell we find that the cavity is completely filled with cytoplasm, near the center of which lies the conspicuous nucleus (Fig. 3, A). In the cytoplasm are also numerous very small, rounded and rod-shaped bodies. Some of these bodies are the beginnings (primordia) of structures known as plastids, such as chloroplasts and leucoplasts, to be described more fully in subsequent paragraphs; others, the more minute, whose function is unknown, will be called chondriosomes (mitochondria).

As the cells become older and increase in size before reaching the adult stage, the quantity of cytoplasm may not increase in proportion to the volume of the cell. The increase in size is due largely to the absorption of water, which accumulates in one or more vacuoles.

The result is similar to that seen in the leaf of Elodea, or as shown in Fig. 3, B, *v*. In older cells the cytoplasm becomes spread over the inner surface of the cell, while one or more vacuoles occupy the bulk of the cell cavity, as in the cells of the leaf of Elodea.

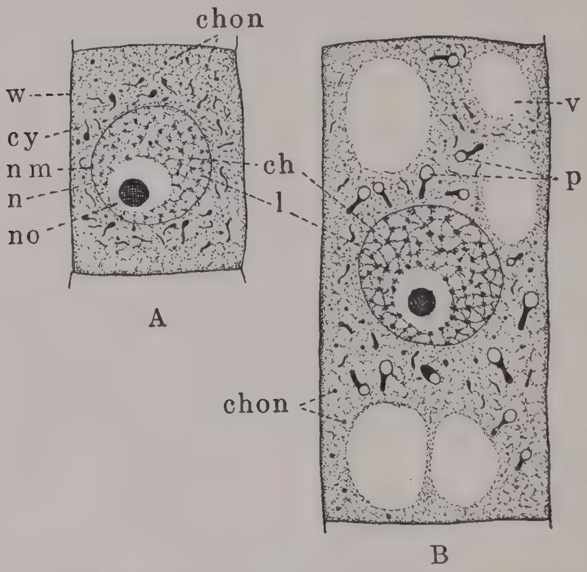

FIG. 3.—Sections of fixed and stained cells from the root tip of the garden pea (*Pisum sativum*). A, young cell before appearance of vacuoles. B, older cell with vacuoles. *w*, cell wall; *cy*, ground work of cytoplasm; *n*, nucleus; *nm*, nuclear membrane; *no*, nucleolus; *ch*, chromatin; *l*, linin; *p*, plastids; *v*, vacuoles; *chon*, chondriosomes. The leucoplasts are in the form of a hand mirror in B, the rounded starch inclusions being colorless.

Structure of the Nucleus.—Turning our attention now to the nucleus, we find that this structure is generally a spherical or elongated body delimited from the cytoplasm by a definite membrane of its own, the *nuclear membrane* (Fig. 3, A, *nm*). Within may be seen one or more globular bodies, the *nucleolus* or *nucleoli*. The nucleolus may lie in a definitely circumscribed area. Distributed throughout the nuclear cavity is a mesh work of very fine threads, the *linin*, upon which are held numerous irregular granules varying in size, the chromatin granules. The chromatin is readily stained by various specific stains, while the linin tends to remain colorless. The rest of the nuclear cavity is occupied by a watery fluid, the nuclear sap (karyolymph).

Division of the Nucleus.—Inasmuch as the nucleus is a permanent organ of the cell, it follows that new nuclei must arise by the division of pre-existing nuclei. There are two methods of nuclear division, namely, direct division, or *fragmentation*, and indirect division, or *mitosis.*

Direct Nuclear Division.—In direct nuclear division the nucleus divides merely by constriction. The resulting nuclei may often be of unequal size. Direct nuclear division occurs only in older cells that have passed into a purely vegetative condition. Such cells have lost the power of growth and division; they do not serve as a starting point for the development of new plants or new organs.

Mitosis, or Indirect Nuclear Division.—The important steps in mitosis may be indicated as follows: In figure 4, A, the chromatin is seen to be distributed upon the linin threadwork in small irregular lumps or granules of varying size. When the chromatin is in this finely divided state, the nucleus is said to be in the *resting* stage. One or more nucleoli may be present. As the process of division progresses, the chromatin granules come to be so arranged as to form a definite cord, or thread, called the chromatin *spirem* (Fig. 4, B). During this process the quantity of chromatin has increased somewhat. In the cells here under consideration the spirem is a continuous thread without free ends.

The spirem now segments transversely into a definite number of pieces known as *chromosomes* (Fig. 4, C). In young, or embryonic, tissue the number of chromo-

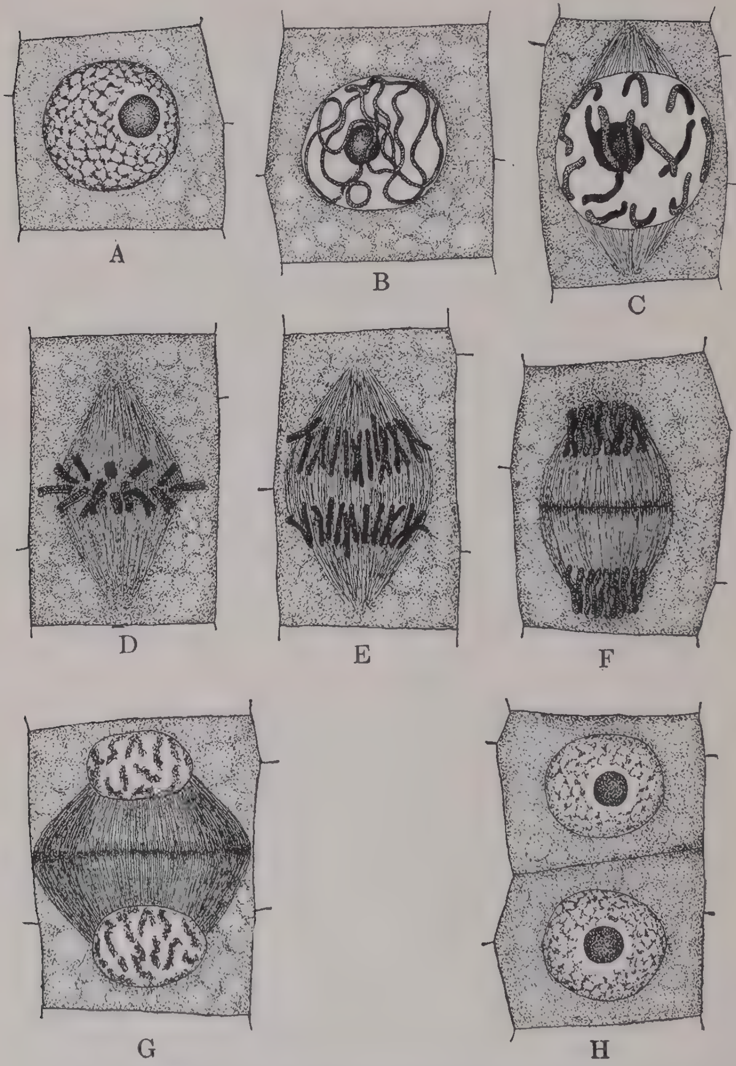

FIG. 4.—Nuclear and cell division in the root tip of the onion (*Allium cepa*). A, the resting stage. B, the spirem. C, chromosomes resulting from cross segmentation of the spirem; caps of spindle fibers on opposite sides of the nucleus. D, the spindle stage; the chromosomes split lengthwise. E, anaphase. F, telophase; the chromosomes have arrived at the poles, and a cell plate has been formed. G, daughter nuclei have been formed, and the cell plate extends across the cell. H, two daughter cells.

somes is usually constant for the species. We thus see that the spirem is composed of a definite number of chromosomes united end to end, and in such a manner that the limits of the individual chromosomes cannot be determined.

During the transverse segmentation of the spirem into chromosomes, or sometimes a little earlier, there appears in the cytoplasm, on opposite sides of the nucleus, a sheaf-like cap or mass of very fine fibers. These are derived from the cytoplasm, and they will give rise to the future spindle fibers (Fig. 4, C, D). About this time the chromosomes are seen to split lengthwise, and the halves of each chromosome thus formed are called daughter chromosomes, or daughter segments. The nuclear membrane now disappears, and the masses of fibers extend across through the nuclear cavity and come together in such a way as to make a sheaf, or spindle. The ends of the spindle, which may converge to a point, are the poles; the transverse plane midway between the poles is the equator. During the formation of the bipolar spindle, the chromosomes are brought into the region of the equator, where they are arranged in a plane and sometimes placed radially like the spokes of a wheel (Fig. 4, D). The chromosomes thus arranged in the equator form the nuclear plate. From each daughter segment (chromosome) a small bundle of spindle fibers extends to the pole toward which that segment is soon to pass. Other spindle fibers extend continuously from pole to pole without being attached to any chromosome. In the meantime the nucleolus has disappeared.

The daughter chromosomes now pass to the poles, one half, going to one pole and the other half to the other pole (Fig. 4, E, F). The two resulting nuclei will consequently have the same number of chromosomes and the same quantity and quality of chromatin material. Such a nuclear division is an *equational* division.

As the daughter chromosomes reach their respective poles, they generally become closely crowded together, and new nuclear membranes are soon formed, thus outlining the two new nuclei (Fig. 4, G). The spindle fibers connecting the two nuclei at this stage are designated the *connecting* fibers. The chromosomes of each daughter nucleus now fragment and reticulate, by the formation of vacuole-like spaces within, into smaller, lump-like, irregular pieces, which are generally connected by slender strands to form a net or *reticulum*. The very fine colorless threads connecting the larger chromatin masses or granules are linin. The breaking up into smaller pieces continues until the chromatin is resolved into finely divided granules held upon the linin threadwork like that of the resting nucleus. In the meantime a nucleolus has appeared in each new nucleus. These new nuclei are the *daughter nuclei* (Fig. 4, G, H).

We may now turn our attention to the nucleolus which was present in the parent cell (Fig. 4, A). During the process of division just described, at or before the spindle stage, the nucleolus disappears as such. A new nucleolus, or nucleoli, reappear in each daughter nucleus, usually closely associated with the chromatin (Fig. 4, H). The author of this book is convinced that the nucleolus represents reserve material which may be used by the nucleus as needed, and especially in connection with the development of the chromatin. In well nourished cells there seems to be more nucleolar material than in cells poorly nourished. In well nourished spore-bearing cells of certain higher plants (Lilium) when one or more large nucleoli were present in the nucleus, many small nucleoli are observed scattered throughout the cytoplasm during mitosis. This seems to indicate that the nucleoli are either dissolved or broken up into smaller parts.

Types of Cell Division.—Of the various types of cell division, and their modifications, the following will be described: division by cell plates, constriction, cleavage furrows, and internal cell division.

Division by Cell Plates.—Division of cells by means of cell plates is the commonest and most widely occurring form among plants. An excellent illustration is to be found in young tissues, such as the growing end of roots, and we shall select the root of the onion, as in the case of nuclear division.

When, as seen in Fig. 4, F, the daughter chromosomes have reached the poles of the spindle, and during the formation of the daughter nuclei, a transverse line appears in the equatorial region of the connecting fibers (Fig. 4, G).

This line, which is the edge of a disk, is the *cell plate.* It begins as a small, circular disk at the center of the system of connecting fibers, and progresses in all directions until it meets the plasma membrane of the cell. The cell plate is of the nature of a plasma membrane. It splits, forming two plasma membranes, between which the cell wall is laid down (Fig. 4, H). In this type of cell division, therefore, the cell-plate is formed by the connecting fibers.

Division by Constriction.—Division by constriction is found in certain algae, as in the common Cladophora. It occurs also in groups of plants widely separated in relationship. In this form of division cell plates are not present. In fact, nuclear and cell division occur at different times. The process is made clear in fig. 5, A-C. At a point usually midway between the ends of the cell, the cytoplasm is seen to be pushed away from the lateral wall of the cell as if constricted. At this constriction a new transverse wall is being built up by the cytoplasm in the form of a ring. The constriction becomes deeper, and the new wall broader, progressing toward the center (Fig. 5, B). The new transverse wall is now a circular disk with a circular opening in the center.

Finally the disk is completely closed, and the new wall is complete (Fig. 5, C). The wall layer of cytoplasm soon moves out into the corners of the respective cells.

This mode of cell division occurs in a slightly modified form in Spirogyra. In this plant, however, the division of the cell follows the division of the nucleus, since the cells are uninucleate.

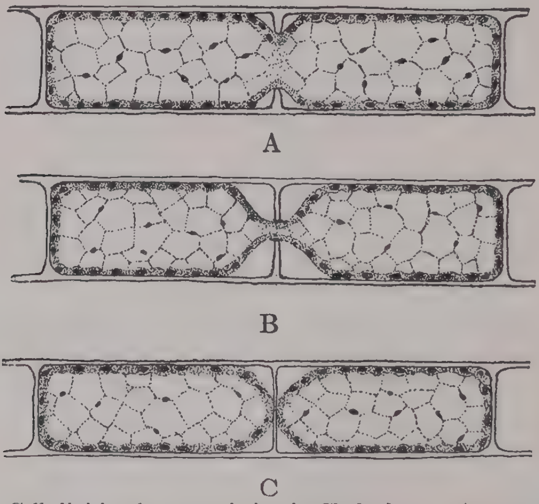

Fig. 5.—Cell division by constriction in Cladophora. A, transverse constriction of cytoplasm near middle of cell, and beginning of transverse ring of new wall. B, further progress in division. C, division complete.

Division by Cleavage Furrows.—Division by cleavage is accomplished by means of surface furrows that begin at the plasma membrane and at the vacuoles. They meet and divide the common cytoplasm up into portions containing one or more nuclei. An illustration is found in the large cell which bears spores in certain common moulds. This is a multinucleated cell (Fig. 6, A). Proceeding from the periphery of the cell and from vacuoles, the furrows divide the cytoplasm into numerous cells (Fig. 6, B). Certain details of the process are shown

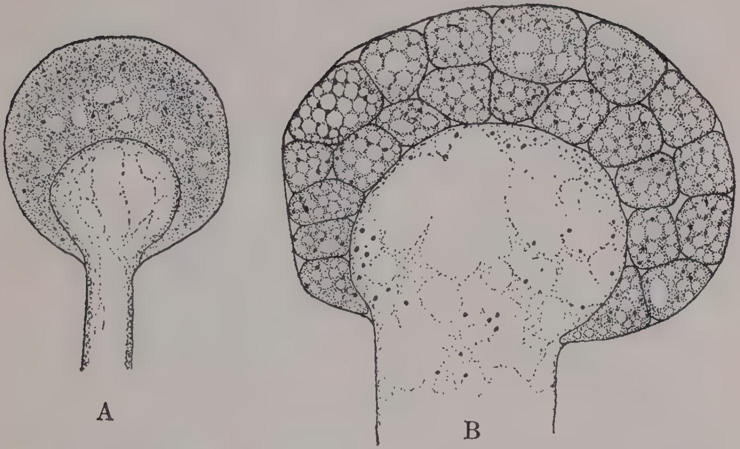

Fig. 6.—Cell division by cleavage furrows. A, young sporangium of common mould, consisting of a large multinucleate cell, the dots representing the nuclei. B, sporangium of a mould (*Sporodinia grandis*) divided into rounded cells by surface cleavage furrows. (B, from Harper.)

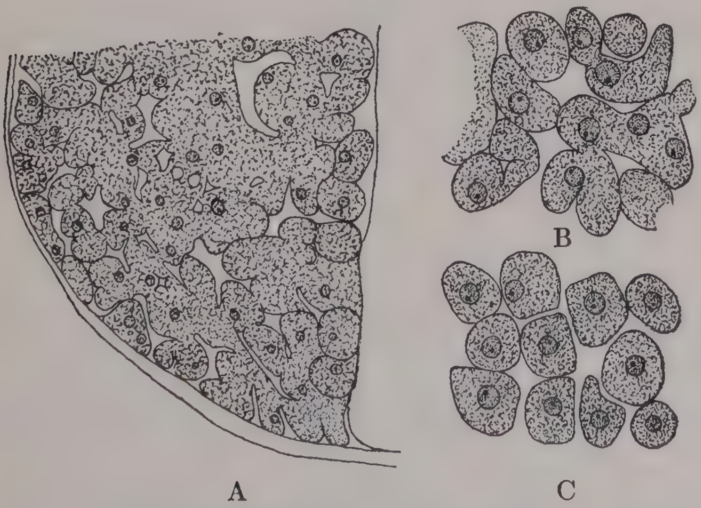

Fig. 7.—Cell division by cleavage furrows. A, portion of a developing sporangium of a mould (*Pilobolus crystallinus*) showing how surface furrows meet those from vacuoles, cutting the mother cytoplasm into large irregular masses. B, further cleavage of these masses. C, the cells finally resulting from the progressive cleavage. (From Harper.)

in fig. 7. In fig. 7, A, which is a portion of the initial cell, surface cleavage furrows extend into the cytoplasm, meeting vacuoles in such a manner that the entire cytoplasm of the large cell is divided up into large irregular portions containing from one to several nuclei. In these masses cleavage continues until the large initial cell is divided into the ultimate cells (Fig. 7, B, C).

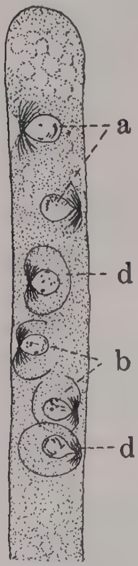

Fig. 8.—Internal cell division. Portion of a young spore sac (ascus) of the cup fungus, *Lachnea scutellata*, in which the cells are delimited from the mother cytoplasm by the action of the persisting spindle fibers attached to the nuclei. *a*, nuclei with attached fibers; *b*, cell partly delimited; *d*, *d*, cells completely formed. (From Harper.)

Free Cell Formation.—Free cell formation consists in the cutting out, or delimitation, of cells from the common cytoplasm of the given cell by the activity of spindle fibers that persist in connection with the nuclei. As an illustration we shall select the initial cell of the spore sac (ascus) of a common cup fungus.

Here, as seen (Fig. 8), the spindle fibers, or polar radiations, attached to the nuclei curve round outward and backwards to form plasma membranes, thus cutting out cells from the mother cytoplasm.

PLASTIDS

Certain bodies occurring in the cytoplasm, that are centers of chemical activity concerned chiefly with the building up of compounds, are known as plastids.

Chloroplasts.—Among the plastids in the cell the most conspicuous, and probably the most important, are the *chloroplasts*, which contain the green pigment *chlorophyll*, and which build up starch by the process of photosynthesis. Because of this fact, the starch formed in the chloroplast is called photosynthetic starch.

In the higher plants chloroplasts are usually small, globular, oval, elongated, or polygonal, if crowded; but in some of the algae (pond silks) they are larger in

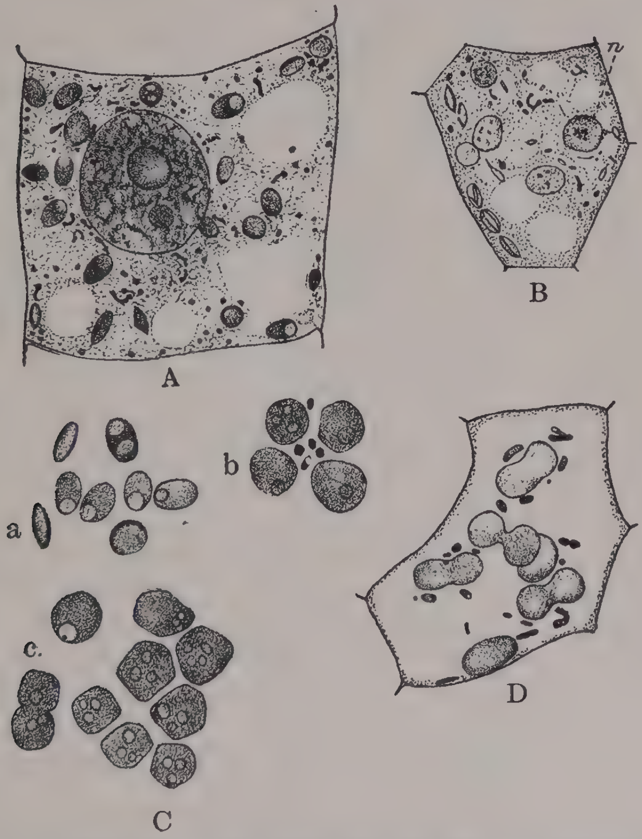

Fig. 9.—Development of chloroplasts from primordia. A, cell from hypocotyl of embryo of the pine (*Pinus banksiana*) with young chloroplasts and very small, round, and rod-shaped bodies; B, cell of meristematic tissue of liverwort (Marchantia) with chloroplasts in different stages of development; C, developmental stages in young seedling of Pinus; D, older cell of Marchantia in which fully developed chloroplasts are dividing.

proportion to the size of the cell, and few in number, and of various shapes, such as tabular, spiral, cylindrical, cup-shaped, or star-shaped. Each chloroplast may contain one or more starch inclusions (Fig. 9, A, B).

Structurally the chloroplast consists of a firmer framework, the *stroma,* which contains the pigment, chlorophyll. The center of the stroma is less dense, or somewhat vacuole-like, while the firmer periphery is porous. The pigment is held in the porous peripheral portion.

In embryonic cells, and in young meristem, chloroplasts, and other plastids as well, arise from very minute, granular, or rod-shaped beginnings termed *primordia.* The rod-like primordia are either straight, curved, or comma-like, or club-shaped (Fig. 9, A, B, D). There is much evidence to support the belief that the primordia divide by fission, and that they are permanent organs of the cell. In the development of the chloroplasts in meristematic tissue the primordium increases in size, becoming rounded, lenticular, or sometimes club-shaped. The less dense center can be readily seen in stained cells. In it the starch inclusion accumulates. Fig. 9, C, *a*, *b*, *c*, shows several steps in the development of the chloroplast from the primordia in a very young seedling of pine.

The adult, or full grown, chloroplast is capable of division by constriction (Fig. 9, D). In this respect adult chloroplasts differ from other plastids.

Chlorophyll.—As stated in the foregoing paragraph, the green color of the chloroplasts is due to the presence of the pigment, chlorophyll. A few simple experiments will throw some light on the nature of this pigment. If some fresh leaves that are not too old, or a quantity of some suitable alga, are first steeped in hot water, and then, after draining off the water, are kept in alcohol for an hour or longer, the green color will be dissolved in the alcohol, and the plant material will be left colorless. If the cells are now examined with the microscope, the stroma of the chloroplast will be seen as before treatment, though colorless.

An alcoholic extract of chlorophyll, when observed by transmitted light in a test tube or other glass vessel, appears a clear, deep green. In reflected light, as when examined against a dark background, it appears a dark purple, due to a sort of fluorescence. If the extract be kept in a cool, dark place, the chlorophyll may remain unchanged for a few days, but, if exposed to direct sunlight for a few minutes, it will be quickly decomposed, as indicated by the disappearance of the green color and the appearance of a dark, smoky color. The instability of chlorophyll may be shown in various other ways.

That the chlorophyll in the alcoholic extract contains different pigments may readily be demonstrated by diluting a small quantity with water and adding benzol. In a short time the benzol rises to the surface of the mixture as a sharply defined, deep green layer, while the alcohol and water below will be of a pale straw color. The green pigment at the top is chlorophyll green, and the yellowish pigment below is chlorophyll yellow. The latter is composed of two pigments, the orange-colored *carotin*, and the lemon-yellow *xanthophyll*. Chlorophyll green is composed of two pigments, *chlorophyll a*, which is a deep, blue-green, and *chlorophyll b*, a lighter green. Chlorophyll is composed of carbon, oxygen, hydrogen, nitrogen, and one metal, magnesium.

If growing plants are kept in the dark, the chloroplasts will appear yellowish, owing to lack of chlorophyll green. The yellow pigment, under this circumstance, is spoken of as *etiolin*. Barring some exceptions, light, therefore, is necessary to the development of chlorophyll. In the seeds of pine, and of some other plants, the chloroplasts become green in darkness, or with the aid of whatever light may penetrate the seed coat.

Autumnal Coloration.—Autumnal coloration of the leaves of many deciduous trees, such as the maples and others, is due largely to the decomposition of chlorophyll and other substances in the cells. When the leaves cease to function, and most of the food substances are removed through decomposition in the leaf, or through translocation to other parts of the plant, the chlorophyll green may be decomposed, leaving the carotin and xanthophyll in the plastids. The result is a pure yellow color. However, decomposition may extend to the yellowish pigments as well. Finally in many leaves red and purple pigments (anthocyanin) are formed which impart the wonderful reds and purples to the autumnal landscape. These pigments may then be taken up by the solid parts of the cells, and the color is preserved when the leaves are dried and kept away from direct sunlight. The brown color of beeches and oaks is due largely to the presence of tannin.

Other Pigments in the Plastid.—In certain groups of plants other pigments occur in the plastids along with chlorophyll modifying the green color or obscuring it completely. In many of the blue-green algae the additional pigment is *phycocyanin*, which imparts the bluish color to the cells, while in the red algae the additional red pigment is known as *phycoerythrin*. These two pigments are soluble in water and present a characteristic fluorescence in reflected light. The brown color in the brown algae (Phaeophyceae) has been attributed to the additional brown pigment, *phycophaein*. There is some difference of opinion as to the presence of chlorophyll in the brown algae, it being maintained that only one pigment, *fucoxanthin*, is present, which is closely related to chlorophyll. The characteristic color of the chloroplast in Diatoms is held by some authors to be similar to that in the brown algae, while others regard it as partaking of the nature of carotin. The name, *diatomin*, has also been applied to it.

Pigments Dissolved in the Cell Sap.—Pigments, chiefly blues and reds, occur in the cell sap of various plants, imparting those colors to the parts containing the pigments. They are known as *anthocyan*, or *antho-*

cyanin. Thus the red color of a rose or the blue color of a violet is due to anthocyanin. The yellow pigment, xanthophyll, occurs in the petals of some flowers, as the yellow tulip. This pigment is regarded as being produced by numerous small, round, or rod-shaped plastids, each plastid forming a tiny droplet of yellow fluid. The droplets finally run together and collect in the cell sap. It is not at all improbable that anthocyanin is a product of definite living plastids, rather than a chemical combination produced in the cell sap as a mother fluid.

Leucoplasts.—In parts of plants into which light does not penetrate are found colorless plastids that build up starch also. This starch is known as storage starch, inasmuch as it is stored food and as it is made from the starch or other carbon compound originally manufactured in the chloroplasts. An illustration will serve to make this statement clear. In the leaves of the potato plant, for example, starch is made by the chloroplasts. This is photosynthetic starch. This is changed to a form of sugar (glucose) and transported from the leaves, through the stem, to the tuber under the ground. The leucoplasts in the cells of the tuber change the glucose into starch. The changing of glucose into starch by the leucoplast does not require light as a source of energy.

Origin of Leucoplasts.—Leucoplasts, like chloroplasts, are derived, in embryonic cells, from small, granular or rod-like primordia, as shown at *p* in Fig. 3 and in Fig. 10, A, B. In the transformation of the leucoplast from the rod-shaped primordium in the root of the common pea, this body increases in size, and, either near one end or in the middle, an enlargement appears containing a substance giving a starch reaction (Fig. 10, B). Two or more starch inclusions may be formed in a developing primordium, as in Fig. 10, C. In cells of the root cap each leucoplast contains a relatively large starch grain, the plastid covering the starch as an extremely thin layer, thickened, however, in the form of a crescent at one side (Fig. 10, A, *st*).

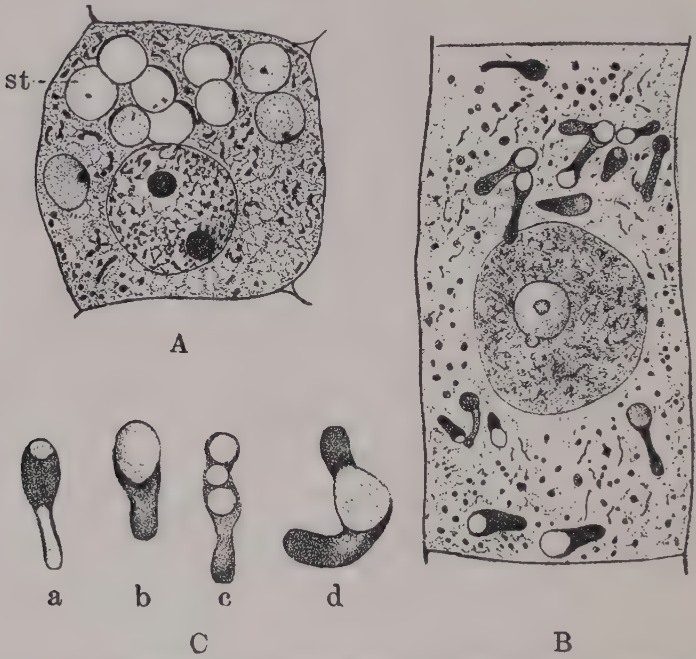

Fig. 10.—Development of Leucoplasts in the root tip of the garden pea (*Pisum sativum*). A, cell from root cap with several starch grains, *st*, in which the plastid appears as a dark, narrow crescent at one side of the colorless starch grain; the larger straight or curved, rod-shaped bodies are probably plastid primordia and the very small round granules are regarded as chondriosomes; B, cell from meristem of root with leucoplasts in different stages of development; C, *a*, *b*, *c*, *d*, leucoplasts with starch inclusions, three inclusions being present in *c*.

Similarity of Chloroplasts and Leucoplasts.—Chloroplasts and leucoplasts are morphologically alike; that is, (1) they originate from primordia that cannot be distinguished from one another in young cells; and (2) when exposed to the light, leucoplasts may develop chlorophyll and become green (Fig. 11). This fact can be demonstrated by exposing young potato tubers to the light. In the outer parts the leucoplasts will become green. It happens also that chloroplasts in certain parts of the plant may function as leucoplasts, as in the cells at the base of the leaf of Elodea.

Chloroplasts, however, can multiply by division in the mature, or adult stage, while leucoplasts cannot do so when mature. The activity of leucoplasts is confined chiefly, though not exclusively, to older cells that have passed into a permanent vegetative condition.

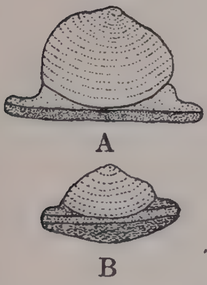

Fig. 11.—Leucoplasts with starch grains, from surface tuber of *Phajus grandifolius*, an orchid. B, the plastid has become green, illustrating the change from leucoplast to chloroplast. (From Strasburger.)

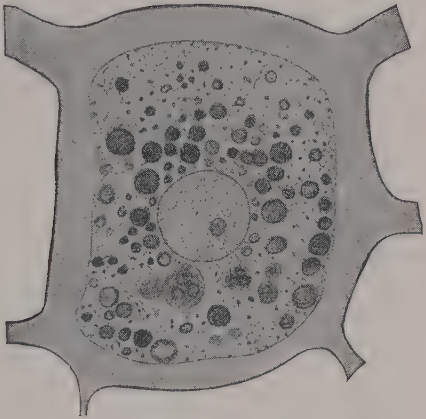

Fig. 12.—Cell of the aleurone layer of a grain of corn, showing the aleurone granules in all stages of development from the primordia.

Protein Plastids and Other Plastids.—Protein plastids may be readily observed in the outer, or aleurone, layer of the endosperm of certain seeds such as those of Indian corn. Here they are seen in the form of conspicuous globules, which may be colorless or variously colored, as in the corn with blue endosperm (Fig. 12). They arise from small primordia.

The oil in the seed of the castor oil plant (Ricinus) is derived, presumably, from oil plastids. These may be morphologically similar to leucoplasts.

Chromoplasts.—Chromoplasts are definite bodies occurring in many cells containing certain pigments. A good example is seen in the sepals of the common garden nasturtium (Tropaeolum) or in the root of the carrot (Fig. 13).

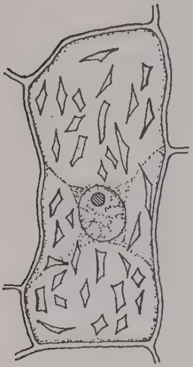

Fig. 13.—Cell with chromoplasts from the upper side of a sepal of yellow flower of Nasturtium (*Tropaeolum majus*).

Cell Inclusions.—The substances built up by plastids, such as carbohydrates, oils, fats, and proteins, are often referred to as inclusions of the cytoplasm. In addition to these are mineral crystals of various composition. They are very abundant in stems and leaves of many plants.

The Cell Wall.—When the structure of the firmer parts of especially the higher plants is taken into consideration, the most outstanding feature is the cell wall. In only a very small part of a tree or woody bush do the cells possess living protoplasm, the bulk of the plant being composed of the walls of cells from which the living substance has almost wholly or quite disappeared. In cells of all plants, the cell wall, if present, is dead material, which was, of course, built up by the living substance; it is the house in which the living occupant dwells.

In both high and low forms the walls between neighboring cells in certain individuals, or in certain parts of those individuals, are perforated by small holes, *pits*, through which delicate threads of cytoplasm (plasmodesmen) extend from one cell to another (Fig. 14). In this manner the cells of certain tissues are in direct cytoplasmic communication with each other. In certain plants, such as red sea-weeds, the cytoplasmic connections between cells are large and easily demonstrated. It should be remembered, however, that all living cells of plants are not connected by living substance, and the whole plant cannot be regarded as a continuous plasmodium.

The primary walls of cells are usually thin and delicate. As the cells mature in many tissues, the walls become very thick owing to the formation of secondary thickening layers (Fig. 15). The secondary thickening is accomplished by the deposition of successive layers of cell wall substance, or by the intercalation of new particles of cell wall between those already present.

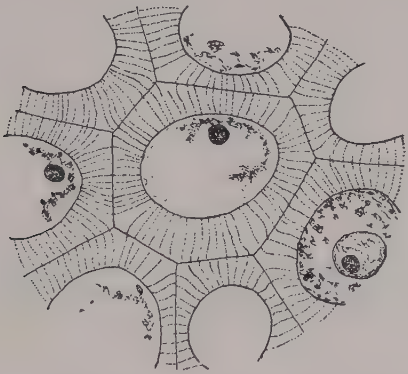

Fig. 14.—Cell of the endosperm of the persimmon (*Diospyros discolor*) with portions of adjacent cells, showing the numerous fine cytoplasmic connections (plasmodesmen) that pass through the pits of the thick walls.

The Middle Lamella.—The middle plate in walls of neighboring cells of mature tissue is of a different composition from that of the secondary thickening, and this middle plate is the *middle lamella*. This fact is clearly shown in Fig. 15, *a*. When intercellular spaces are not present, the middle lamella is much thickened at the angles of the cells, as shown by the gusset-like thickening at *b*. The middle lamella occupies the position of the primary wall of young cells, but it is not the primary wall alone. The primary wall has undergone changes due to the infiltration and addition of various other substances. The middle lamella is soluble in reagents that do not readily dissolve the secondary thickening of the walls. For example, a mixture of chlorate of potash and nitric acid will dissolve the middle lamella, while the secondary thickening is more resistant. On the contrary, sulphuric acid readily dissolves the secondary thickening, but not the middle lamella. The maceration of tissues is accomplished, therefore, by the softening, or dissolution, of the middle lamella. The rhetting of flax in the field is brought about by the dissolution of the middle lamella as a result of decay or oxidation.

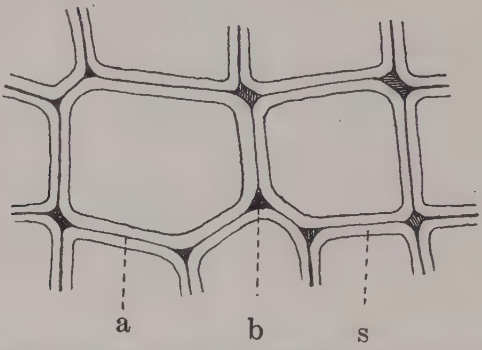

Fig. 15.—Cells of pine wood, showing middle lamella, *a*, *b*, and secondary thickening, *s*,

The varied character of cell walls is not due wholly to differences in thickness or configuration, but to their chemical composition as well.

Cellulose.—The fundamental substance in cell walls is cellulose,* which chemically is a carbohydrate with the formula $(C_6H_{10}O_5)_n$. The walls of the pith of the elder, the pith of the sunflower, and the fiber of the cotton plant are examples of a rather pure cellulose. It is to be understood that cellulose exists in various forms. In seeds of the date and other palms a form of cellulose constitutes the reserve food. This is easily digested when the seed germinates, but in the dried form it is hard and stony, sometimes being spoken of as "vegetable ivory." Cellulose turns blue upon the application of chlor-zinc iodine or iodine and sulphuric acid.

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* Cell walls of fungi are composed of a modified cellulose, which in some respects bears a resemblance to animal chitin.

Pectose, Pectine.—Cell walls are rarely composed of pure cellulose. The middle lamella, for example, contains in addition to cellulose pectic substances such as pectine and pectose. Pectic substances are abundant in the tender cell walls of such fruits as quinces, apples, pears, currants and gooseberries, and in fleshy roots of some vegetables as carrots and parsnips. Pectine and other pectic substances are soluble in water, and when dissolved in concentrated solutions they set into jellies on cooling. Characteristic stains for cells walls containing pectine and pectose are ruthenium red and haematoxylin, the former giving a rose and the latter a blue color.

Cell walls may contain other substances in addition to cellulose such as lignin, cutin, and suberin. These will be referred to later in connection with tissues whose walls they characterize.

Protoplasm.—The term protoplasm as used in this book is applied to all the living substance in the cell; it includes, therefore, nucleus, or nuclei, and cytoplasm, together with specialized parts, as plastids and plastid primordia. Inclusions such as starch, sugars, oils, fats, mineral crystals, and other demonstrably inert bodies do not represent living substance. The following remarks refer chiefly to the cytoplasm.

When seen with the microscope, cytoplasm in live cells appears as a thick, viscid substance of the consistency of glycerine or strained honey at room temperature. The ground substance, including the plasma membrane lying next to the cell wall, is colorless and homogenous. The plasma membrane and a layer of variable thickness lying next within the membrane is of firmer consistency and always stationary. The inner mass of cytoplasm is more fluid, and grayish granular in appearance, owing to the presence of numerous small, opaque bodies such as plastid primordia and other small granules whose character is not known or not well understood. When cytoplasmic movement is observed, it is this more fluid portion that is in motion. The movement is recognized by the change in position of the visible granules, or by the movement of larger plastids and other bodies located in the parts that are in motion.

In composition, protoplasm is made of water and solid substance. Of the dried substance, one-third to one-half is protein, the remainder being composed of fatty bodies, sugars, and other carbohydrates, organic acids and bases, and salts of potassium, magnesium, calcium, sulphur, phosphorus, etc. The chemical structure of protoplasm is not known. It is admittedly very complex. Any attempt to indicate by a chemical formula a molecule of protoplasm would be useless from our standpoint.

The botanist knows protoplasm chiefly from observations of its visible structure, and from its various physical and physiological manifestations. Protoplasm is capable of absorption, digestion, assimilation, and excretion; it is automatic and sensitive, or irritable; that is, it is capable of responding to stimuli; it has the power of growth and reproduction. By saying that it is automatic, we mean that its source of activity comes from within. Protoplasm grows, not as a crystal, by the addition of material to the outside, but from outside materials taken within and there converted into its own substance. It is the only known substance that can reproduce itself, and only living protoplasm can produce other living protoplasm.

Many of the phenomena of living protoplasm, such as the splitting of chromosomes and the dividing of chloroplasts, cannot at present be explained in terms of physics and chemistry. Mechanistic explanations as known at present are insufficient.

Colloidal Character.—It was stated in the foregoing that protoplasm is a fluid. In order to gain some knowledge of the kind of fluid represented by protoplasm, certain fundamental facts concerning fluids in general may be useful.

When a lump of sugar is dissolved in water, the particles of sugar become dispersed to the fineness of the molecule. If a lump of salt be thrown into the water, the particles of salt will not only disperse to the fineness of the molecule (NaCl), but dispersal will continue even beyond this so that some of the molecules are separated into the elements, sodium (Na) and chlorine (Cl). These two elements are then said to be dissociated. The elements of the sugar molecule do not become dissociated in water. In either case we have, however, a perfect, or homogenous, solution. The substance dissolved, in this case salt or sugar, is spoken of as the *solute*, and the medium of dispersal, which in this case is water, is the *solvent*. Substances like sugar, salt, etc., which crystallize on solidifying from a solution, are called *crystalline* substances, and they are said to represent the crystalloid condition. If, on the other hand, glue or gelatin, for example, be dissolved in water, it will be found that these bodies do not dissolve down to the molecule, or, if so, rarely beyond the molecule. The ultimate particles of dispersal are usually larger than the molecule. Such solutions are said to be *imperfect*, or *heterogeneous* solutions.

If perfect solutions, such as those of sugar or salt, be examined with the ultramicroscope, they will appear perfectly clear, while a dilute solution of glue, clear to the naked eye, when thus examined with the ultramicroscope, reveals numerous small particles floating in the fluid, just as particles of dust are seen in the air when a beam of light is admitted to a darkened room.

Such bodies as glue, gelatin, and the like, which do not crystallize on solidifying from solution, are called *colloids.* Certain substances may sometimes exist in the crystalloid and sometimes in the colloidal condition. The conclusion is that colloid and crystalloid represent different conditions of diffusibility. Diffusibility, therefore, is regarded as a *condition* of matter when minutely subdivided, or in solution in some liquid, as contrasted with its state or condition when existing alone. The *state* of a substance may be gaseous, liquid, or solid; its *condition,* when in solution, may be either crystalloid or colloid. When it is said, for example, that enzymes are colloids, the meaning is that enzymes exist in the colloid condition, and not that enzymes represent a definite kind of substance having the group name *colloids.*

Meaning of the Term, *Phase.*—When the particles of a substance are distributed through the mass of another substance, the mixture represents a *two-phase system,* composed of the *disperse phase,* or substance, and the *continuous phase,* the latter being the medium of dispersal. When the dispersal medium is a liquid, and the disperse phase a gas, a *foam* results; when the disperse medium is a liquid and the disperse phase a liquid, an *emulsion* results, as when finely divided particles of oil are dispersed in water or other fluid. If the disperse phase be a solid, and the medium a liquid, we have a *suspension.* When the colloidal mixture is in the form of a fluid and mobile, it is known as a *sol;* when it is a semi-solid, it is called a *gel.*

If two or more substances are independently dispersed in a common medium, and the behavior of each is independent, there may exist not only a two-phase system, but a poly-phase system.

In a general way, some of the important differences between the crystalloid and the colloid condition may be indicated in the following table:

Crystalloid	Colloid
Crystallize on solidifying	Does not crystallize on solidifying
Disperses to the molecule or further	Does not disperse to the molecule
Osmoses readily	Does not osmose readily
Boiling point higher than that of the solvent	Boiling point about the same as that of the solvent
Does not form a gel	Forms a gel
In molecular motion	In Brownian movement

In applying these very elementary concepts to the living substance in the cell, it may be said that protoplasm constitutes a polyphase emulsion colloid. It must be borne in mind that the cell sap, which is not living protoplasm, together with dissolved crystalline substances is something different from the firmer framework of protoplasm that remains when cells are killed and dehydrated. The firmer framework of protoplasm is chiefly in the form of gels. The plastids, chromatin, and chromosomes, the nucleolus, the spindle fibers, the plasma membrane, and the denser cytoplasm lying next to it, are gels. The more movable parts doubtless represent a sol, or sols, while lipoid substances may be in the form of emulsions.

Such parts of the protoplasm as plastids, chromosomes, and the nucleolus, which may be seen in the living cell with the aid of the microscope, and whose independent existence and behavior can be traced through their different transformations are more readily conceived as gels, inasmuch as the independent existence of each is observable as a semi-solid, or jelly-like, body. Beyond these elementary conceptions we do not find it profitable to go, for the principles of physics and chemistry do not, at present, suffice for the explanation of many of the manifestations of living protoplasm.

Protoplasm differs from the materials with which the physicist or the chemist works in one profound respect: it is alive, and it is the only substance known that manifests life. Its manifestations of life are perceived objectively through its sensitiveness, or irritability, and through its growth and reproduction. The power of growth and reproduction and response to stimuli all come from within, and not from the environment, although these manifestations may be modified by surrounding energy. In short, protoplasm is automatic, and the thing which makes it automatic is the fundamental principle of growth and development that we call life. Attempts to explain the manifestations of protoplasm, which do not employ the materials and methods known to science, pass into the realm of purely abstract or subjective speculation.

Movement of Protoplasm.—Having thus learned something of protoplasm as a fluid, we may now turn our attention to certain movements to be readily observed within cell walls, and in naked cells, or in naked masses of protoplasm.

In such cells as those of the leaf of Elodea mentioned in the beginning of this chapter, or in suitable cells of the Eel-Grass, Vallisneria, or the algae, Chara or Nitella, protoplasmic movement within closed cells may be easily recognized by the fact that the chloroplasts, or other large masses of granular matter, are carried along. In cells of Elodea, for example, the character of the movement is indicated by the chloroplasts which are located in the inner layer of cytoplasm. These are seen to pass down one side of the cell, glide around across the end, and return along the other side. Continuous movement in this manner is known as *rotation.* It is evident that there are two lines in the cell, on one side of which the protoplasm moves in one direction, and on the other side in the opposite direction. This is the neutral line. The neutral line is very evident in cells of Nitella, in which the chloroplasts are stationary, being located in the dense, immovable layer nearer the plasma membrane. The neutral line appears as a clear strip owing to the absence of chloroplasts. In Nitella, as well as in the other plants, the nucleus is carried along in the moving cytoplasm.

Among higher plants a different kind of protoplasmic movement generally prevails. In the cells of the stamen hairs of the Spider-wort (Tradescantia), or the epidermal hairs of the squash, the cytoplasm is not only arranged in a wall layer, but several strands may traverse the large central vacuole. Careful observation will reveal the fact that cytoplasmic streaming may be going on in two or more directions in the cell at the same time. Movement which is going in one direction in a given strand may in a short time be reversed. This form of movement has been called *streaming*, or a circulatory movement.

Certain lower plants, and the reproductive cells of lower, as well as some of the higher, plants, have the power of locomotion, due to the movements of very slender cytoplasmic threads, known as cilia, which lash the water in a definite manner. The motion of cilia is styled *ciliary* movement. Another form of protoplasmic movement is observed in such naked cells as the animal, Amoeba, or the plasmodium of slime moulds. Here the mass as a whole, or in part, moves by a flowing or creeping movement, the *ameboid* movement.

Protoplasmic movements, though automatic, are influenced, or completely inhibited by factors in the environment. Cold retards, and heat accelerates, movement within certain ranges. Observations carried out by the author on cells of the leaf of Vallisneria showed that from 0 to 13° C. movement was nil or very slow. The rate increased with the rise of temperature to the maximum reached at 38°. With further increase in temperature the rate of movement decreased until it ceased at 49°.

If cells in which movement is going on be anaesthetized by means of chloroform, or ether, movement will cease. In general movement will not occur in cells deprived of oxygen.

CHAPTER II

THE LEAF

In presenting the structure of higher plants we shall deal with the important tissues as they appear in types of leaf, stem and root, and explain their development from the primordial meristems. Following the anatomical study each organ will be considered from a more general and comprehensive view point.

THE LEAF

External Morphology of a Foliage Leaf.—A foliage leaf may consist of the blade, *lamina*, the stalk, or *petiole*, and the somewhat enlarged attachment, the leaf *base*. At each side of the base may grow out appendages, the *stipules*. Stipules are very frequently absent. Leaves having no perceptible petioles are said to be sessile.

Venation.—The principal veins of leaves may be arranged in one of two ways, *parallel* and *netted*. In parallel-veined leaves the veins run parallel from one end of the leaf to the other. This type of venation is characteristic of most monocotyledonous plants. If the veins are branched, and the branches anastomose, a net-veining results. This type is common to dicotyledonous plants. In certain net-veined leaves the prominent vein running up through the middle of the blade is known as the mid-rib. When the branches extend from the mid-rib like the divisions of a feather, we have a *pinnately-veined* leaf. If the several large veins reach the petiole at or a little below the blade, the leaf is *palmately-veined*.

Forms of the Lamina.—Leaves are *simple* when they have but one blade; *compound* when two or more blades are present, each blade being called a *leaflet.* The leaf of a grass has usually a long blade, a petiole, known as the sheath, which wholly or partly encloses the stem, and a small outgrowth, the *ligule,* where blade and sheath meet.

It may be mentioned here that stipules vary greatly in size, form, and structure. In certain plants the stipules may be large and foliaceous, larger even than the leaflets, as in the garden pea (*Pisum sativum*).

In the tulip tree (Liriodendron), the stipules develop more rapidly than the blade of the leaf and form the protective cover of the bud; in other words such stipules function as bud scales. Stipules develop into spines in the black locust (Robinia), while in the green briar (Smilax) they are long, slender tendrils.

Arrangement upon the Stem.—As to their arrangement upon the stem leaves are alternate, opposite or in circles, whorled. They are generally so oriented that the blades shade each other as little as possible. The aspect of a Virginia Creeper (*Ampelopsis quinquefolia*) spread over the side of a building or upon a tree trunk is that of a striking leaf-mosaic in which the leaflets so fit together as to present a continuous surface of foliage.

Leaves may be oriented in such a way that one surface of the blade faces the light or is more intensely illuminated. In such cases the upper surface, adaxial side, differs both in appearance and structure from the under or abaxial side. It frequently happens that the sides of the leaf blade are parallel with the direction of strong illumination. The iris is an example.

Minute Anatomy of the Leaf Blade.—The typical foliage leaf consists of three great systems of tissue, the *epidermal,* the *ground* tissue, and the *vascular* tissue.

The Epidermis.—The epidermis covers the entire surface of the leaf including the edge and the petiole. It may be readily stripped off and examined from the surface with the microscope. Thus observed the epidermal cells of the under side are irregular in shape, with curved or wavy interlocking sides (Fig. 16, A). Conspicuous structures suggesting button holes are numerous. Each

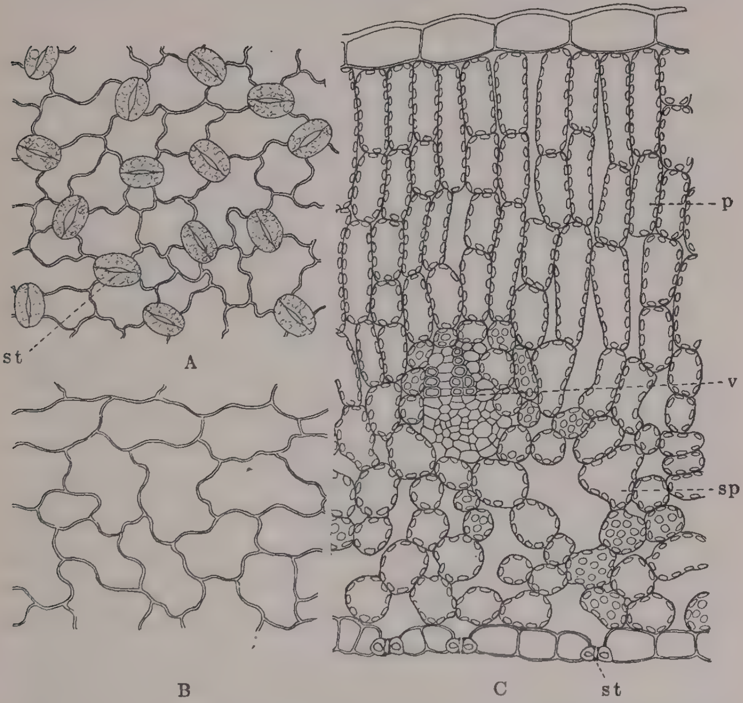

FIG. 16.—Vertical section of the blade of a foliage leaf, and surface views of the epidermis. A, lower epidermis; B, upper epidermis; C, vertical section; *st*, stomata; *p*, palisade cells; *sp*, spongy parenchyma; *v*, cross section of vein (vascular bundle) in which the wood faces the upper and the bast the lower, surface of the leaf.

of these consists of a narrow slit-like opening, or *pore*, formed by two kidney-shaped cells with their concave edges adjacent. The pore is the *stoma* and the two cells forming it are the *guard cells*. The *stomata* form direct communication between the intercellular spaces within the leaf, which are filled with air, and the external atmosphere (Fig. 16, C, *st*). The guard cells may contain numerous, conspicuous chloroplasts.

The guard cells are able to open and close the stoma. In so doing they tend to regulate the interchange of gases, being in reality ventilators. When the guard cells are turgid, more turgid than the neighboring cells, the stomata are opened. If the turgor be equal to that of the neighboring cells, or if, by loss of water, all the living cells of the leaf are less turgid, the stomata are closed. Guard cells distended by water curve outwardly thereby widening the opening; when they lose water they tend to become more straight, and the pore is closed. The increase in sugur content in the guard cells tends to increase their turgidity, and as sugar accumulates in the cells as a result of photosynthesis, illumination tends to lead to the opening of the stomata.

The epidermal cells of the upper surface of the leaf are similar to those on the lower side, but stomata may be entirely absent.

In a vertical section the epidermis is seen as a row of cells somewhat uniform in shape and size (Fig. 16, C). The stomata appear as narrow passages between the outer air and an intercellular spaces beneath. The outer layer of the cell walls consists of waterproofing material, the *cutin*. The radial walls also may be thickened in certain plants, and contain cutin. Such walls are said to be cutinized.

In plants of the desert such as Cacti, Agavas, and others the layer of cutin may be very thick and cutinization may extend to more deeply lying cells.

Cutin.—The outer layer of the walls of epidermal cells of stems and many fruits, with the exception of very young tissues and root hairs, is composed of cutin. As stated cutin is waterproofing material. Its role is not so much to keep the surface dry as to prevent the loss of water by evaporation.

Chlor-zinc iodine turns cutin yellow.

On the surface of fruits and other parts of various plants, as on the stem of sugar cane, there is formed a wax or waxy substance. On the surface of such fruits as grapes, apples, and plums the wax constitutes the "bloom" of the fruit. In the case of the sugar cane wax is especially well developes at the joints, and appears as fine threads or rods standing at right angle to the surface of the epidermis.

Wax is dissolved by such solvents as chloroform, ether, benzene, or hot alcohol.

The Mesophyll.—The ground tissue cells within the epidermis constitute the mesophyll. These are typical parenchyma cells, having thin, soft, cellulose walls. They are usually rich in chloroplasts. The cells near the upper and lower surfaces usually differ much in shape and arrangement. This is not true, however in leaves that stand vertically, and are illuminated equally on both sides.

In the leaf in question, however, the cells beneath the upper epidermis are elongated and stand side by side with their longer axes at right angles to the surface of the leaf. These are the *palisade* cells (Fig. 16, C, *p*). The palisade tissue consists of one to several layers of cells. Between the palisade cells and the lower epidermis is the spongy parenchyma (*sp*).

These cells are irregularly rounded, so that numerous large intercellular spaces occur between them. The intercellular spaces are in communication with each other, and with the outer air through the stomata. It is apparent that the leaf has two surfaces exposed to the air, an *internal* and an *external* surface. The surfaces of all the cells next to the intercellular spaces constitute the internal surface of the leaf.

The cells of the mesophyll bordering upon the conducting cells of the veins make up the *border parenchyma.* They lack chloroplasts.

The vascular system of the leaf make up the veins. The numerous ramifications of the smaller veins anastomose to make an extremely elaborate network. The veins give support to the leaf blade and transport food and water to and from the leaf. From cross sections of the veins it is readily seen that the wood faces the upper surface, while the bast is turned toward the lower side (Fig. 16, C, *v*).

Epidermal Hairs.—In many plants certain cells of the epidermis of both leaves and stems grow out into hairs. The kinds of hairs are almost as numerous as the species of plants. They may be unicellular, varying from small conical papillae to long tube-like structures. Many are extensively branched as in the mullen (Verbascum); others are stellate. In Eleagnus and Sheperdia the hairs consist of scale-like expansions attached at the center by short stalks. Glandular hairs are those that end in a large distal cell which gives out a viscid or sticky substance, as in the Petunia and tobacco plant. The glands on the bud scales of the horse chestnut produce a sticky substance composed of a mixture of gum and resin.*

Anatomy of the Petiole.—Leaf petioles are very variable in form and structure. They may be cylindrical, flattened, grooved, or variously modified into many forms. The vascular bundles are not arranged in a circle, but appear either in a curve as seen in a cross section of the petiole, or their arrangement may be irregular. The tissues outside of the vascular bundles are similar to those occurring in the cortex of the stem.

Origin and Development.—As we have already stated in the introduction, a leaf is an outgrowth of the stem. It arises from the primary meristem as a surface protuberance, the *leaf primordium*. In a longitudinal section of a bud several primordia along with very young leaves in different stages of development may be seen (Fig. 17).

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* It may be noted here that the resin in the pine is not a product of epidermal structures.

At first the growth of the primordium is apical, and in such leaves as those of the fern this mode of growth continues until the adult size is reached. In immature leaves of the Spermatophyta, however, all cells undergo active division and growth.

If the bud in question is to become a dormant or winter bud, the lower or first primordia formed may become scale like, overlap and form a protective covering for the more tender foliage leaves and other structures in the interior. Bud scales afford protection against mechanical injury and from desiccation resulting from freezing and thawing. Under certain circumstances freezing is a drying process.

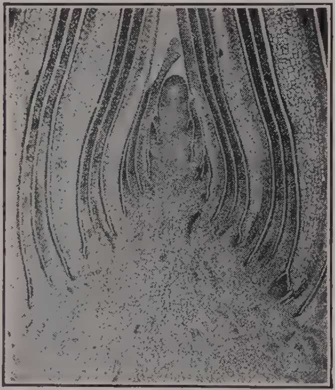

FIG. 17.—Longitudinal section of the growing end of the stem of Indian corn showing primordia of leaves and axillary buds together with parts of older overlapping leaves.

In the case of a foliage leaf growth and differentiation proceeds from the primordia until the adult form and size are reached. The final steps in the process may not occur until after the bud expands and the young leaves unfold. In some leaves as in certain palm trees, the expanded blade may continue to grow near its base after the extremities have begun to die.

Kinds of Leaves.—In the foregoing we have dealt with the general morphology and structure of leaves, holding in mind chiefly the foliage type. During the evolution of the higher plants many modifications have taken place, resulting in a great variety in form, structure and function. These modifications pertain to special functions as correlated with adjustments to the environment.

Reference has been made to scale leaves which constitute the protective cover of winter buds. The term scale leaf is also applied to such food storage parts as the fleshy leaf bases of the underground stem of the onion, and the hyacinth, as well as to many membranous or chaffy structures found in a great many species of plants.

Spore-bearing leaves, *sporophylls*, are those whose exclusive function is to bear spores, although in certain ferns foliage leaves may bear spores, thus combining the production of spores with food making.

The parts of a flower are often referred to as *floral leaves*, although stamens and pistils are primarily spore-bearing structures.

Bracts are the small leaves that subtend flowers. They may be foliar or variously colored.

A spine is morphologically a leaf. The spines of the barberry bush, of the prickly pear (Opuntia) and other cacti are illustrations.

A *leaf tendril* may consist of the whole leaf so transformed or of a part or parts of the leaf. As stated in a preceding paragraph the tendrils of the garden pea are modified leaflets, and those of the greenbriar are stipules.

Many *insect traps* such as those of species of Drosera, the pitcher plants (Sarracenia, Nepenthes) and of the bladderwort (Utricularia) are modified foliage leaves which capture insects and digest parts of their bodies.

The scale-like leaves covering the parts of subterranean buds which develop as aerial stems are known as *cataphylls*. Examples are found in the May-apple, Jack-in-the-pulpit, and in many herbaceous plants having underground stems.

The petiole of a leaf which becomes foliar in character in place of the reduced or absent lamina is a *phyllodium.*

The needle, awl, and scale-like foliage leaves of evergreen Gymnosperms are adaptations to climatic conditions of the temperate zone. They present the minimum surface for the collection of snow and ice.

CHAPTER III

THE STEM

GROWING POINT AND PRIMARY TISSUES

In presenting the structure of stems the following types will be taken into consideration: the type of dicotyledonous plants and gymnosperms, the monocotyledonous stem, and the stem of the fern.

An Herbaceous Type of Dicotyledonous Stems.—The origin of the tissues from the growing end of the stem will be more easily followed with the aid of diagrams of cross and longitudinal sections, as in Fig. 18, A, B, C.

The growing point of the stem is generally a conical or thimble-shaped mass of embryonic tissue, the *primordial meristem.* The cells are thin-walled, isodimentional, each possessing a relatively large nucleus and a dense cytoplasm with no vacuoles; they are always capable of growth and division. From the growing point primordia of leaves and axillary buds arise.

A short distance back of the growing point the primordial meristem is differentiated into three regions, the *protoderm,* which is the surface layer and which will give rise to the epidermis, the *ground meristem,* and the *procambial strands,* several in number. These three regions constitute the *primary meristem.*

The procambial strands are arranged in a circle, and each is completely surrounded by the ground meristem (Fig. 18, B). Each is composed of much elongated cells which are frequently pointed at the ends. In cross section these cells are smaller than those of the ground meristem. The procambial strands give rise to the vascular bundles.

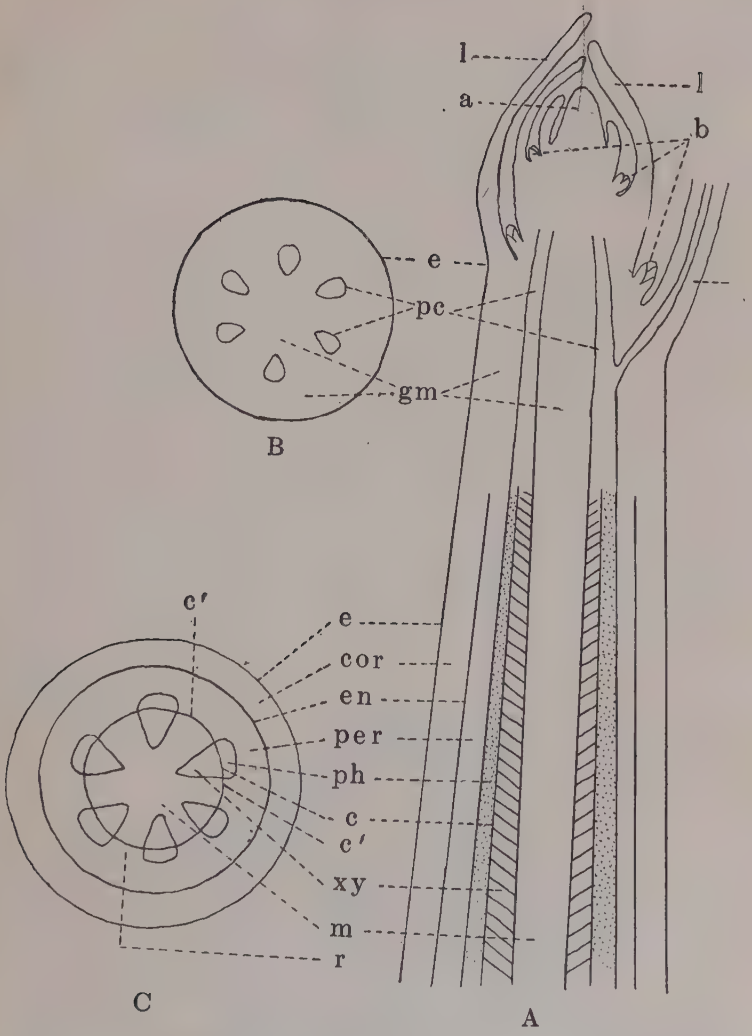

FIG. 18.—A, a diagram of a longitudinal section of the distal end of a dicotyledonous stem. B, a cross section a short distance back of the growing point. C, cross section farther back as indicated. *a*, growing point; *l*, young leaves; *b*, axillary buds; *e*, epidermis; *pc*, procambial strands; *gm*, ground meristem; *cor*, cortex; *en*, endodermis; *per*, pericycle; *ph*, phloem; *c*, fascicular cambium; *c′*, interfascicular cambium; *xy*, xylem; *m*, pith; *r*, primary ray.

In the vast majority of plants the epidermis is but one cell in thickness, the cells of the protoderm dividing anticlinically only, or at right angles to the surface; but in exceptional cases tangential divisions occur also, and a multiple epidermis is the result.

Continuing farther back in the stem, we find that the ground meristem has differentiated into the *primary cortex*, the *pericycle*, the *primary rays* and the *medulla* or *pith* (Fig. 18, A, C). The primary cortex extends from the epidermis to the pericycle. The innermost layer of cells of the cortex is the endodermis. It is located about midway between epidermis and the procambial tissue. The pericycle is the zone of cells extending from the endodermis to the vascular bundles and the outer extremities of the primary rays (primary medullary rays). The primary rays lie between the vascular bundles and extend from the pericycle to the pith.

The pith occupies the central part of the stem.

Each vascular bundle consists of *phloem*, *fascicular cambium*, and *xylem*. The phloem is toward the outside of the stem, while the xylem is next to the pith, the fascicular cambium lying between the two (Fig. 18, A, C, *ph*, *c*, xy).

The location of these several regions and tissues with reference to one another as seen in a transverse section of the wild sweet clover (*Melilotus alba*), is shown in the diagram, Fig. 19, while Fig. 20, is a photograph of the same section.

The appearance of these tissues as seen with the microscope is shown in Fig. 21. Beginning at the outside, the epidermis (*e*) appears as a row of rather uniform cells with outer and inner walls slightly thickened. Stomata are present. Beneath the epidermis is a row of similar cells which will mature as *collenchyma*. The external ridges or buttresses of this stem are composed of collenchyma. A collenchyma, or thick-angled, cell is one

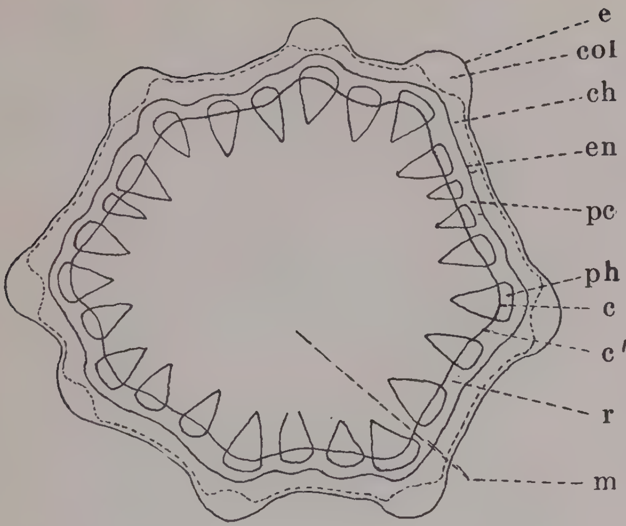

FIG. 19.—Diagram of a cross section of stem of wild sweet clover, *Melilotus alba.* *e*, epidermis; *col*, collenchyma; *ch*, chlorenchyma; *en*, endodermis or starch sheath; *pc*, pericycle; *ph*, phloem; *c*, fascicular cambium; *c'*, interfascicular cambium; *r*, primary ray; *m*, pith.

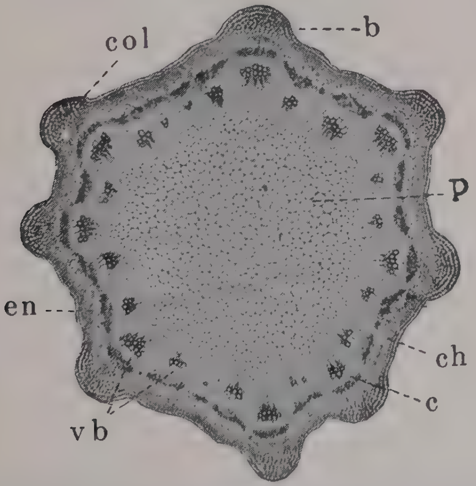

FIG. 20.—Photographmicrograph of a cross section of young stem of wild sweet clover, *Melilotus alba; b*, buttress; *col*, collenchyma; *ch*, chlorenchyma; *c*, fascicular cambium; *v, b*, vascular bundles; *en*, endodermis; *p*, pith

whose walls thicken chiefly at the angles. Collenchyma tissue combines strength with flexibility.

Following the collenchyma is a band of parenchyma cells rich in chloroplasts, the *chlorenchyma* (*ch*). In this region in many herbaceous stems, *sclerenchyma*, or "*stony*" cells, are present. Sclerenchyma cells are short and thick-walled. They impart strength to the region in which they occur. In many plants mineral crystals are present in certain cells of the chlorenchyma. Within the chlorenchyma is the row of well defined cells containing starch, the *endodermis*, or *starch sheath*. Beneath the endodermis is the region of the pericycle (*per*). Here

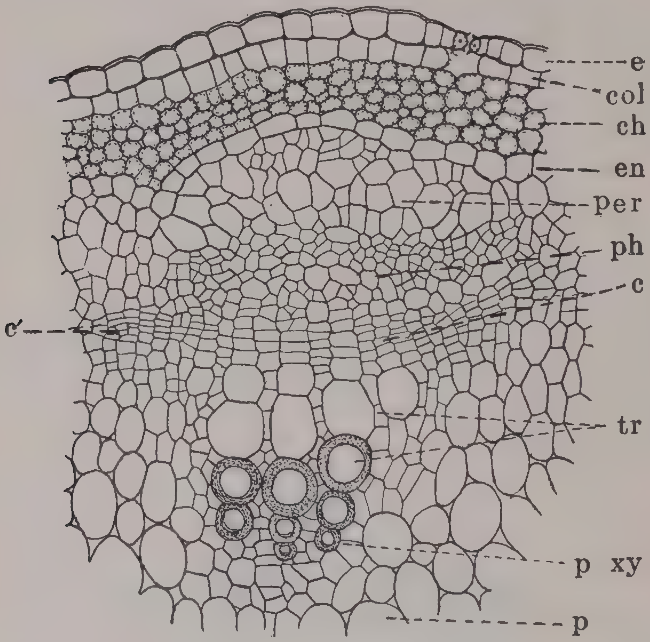

Fig. 21.—Cross section of a portion of the stem of the wild sweet clover (*Melilotus alba*) including a small vascular bundle shown in detail. *e*, epidermis; *col*, collenchyma; *ch*, chlorenchyma; *en*, endodermis or starch sheath; *per*, young bast fibers of pericycle; *ph*, phloem; *c*, fascicular cambium; *tr*, young and old vessels, trachea, of the xylem; *p xy*, protoxylem; *p*, pith.

it consists of relatively large thin-walled cells which will mature as bast fibers. The bast fibers are often more numerous radially opposite the bundles. Following the pericycle is the ring of vascular bundles. The phloem (*ph*) appears as a dense mass of relatively smaller thin-walled cells. Among these, the larger are the sieve tubes, and the smaller cells next to them are the companion cells. The rest of the phloem constitutes the bast parenchyma. The older elements of the xylem are thick-walled vessels and thin-walled parenchyma cells arranged in radial rows. The smaller xylem elements next to the pith make up the protoxylem (*pxy*). The walls of the vessels, wood fibers and tracheids of the xylem contain a characteristic substance, the *lignin*, and such elements are said to be lignified. Thick-walled cells in other regions of the stem may contain lignin.

Phloroglucin and hydrochloric acid gives lignified cells a rose color. They are stained a bright red with safranin.

The fascicular cambium (*c*) between phloem and xylem, and the interfascicular cambium (*c′*) extending across between the bundles form a single layer of meristem, making a complete circle in the stem. The cells of the cambium are very thin walled, and their radial diameters are shorter than the tangential.

The pith is composed of rather uniform thin-walled parenchyma cells with intercellular spaces.

A longitudinal aspect of the elements of a simplified vascular bundle together with those of the pericycle, a few cells of the pith and cortex, is illustrated in Fig. 22.

At the left is the pith (*m*). Following to the right are the annular and spiral vessels (*s*) of the protoxylem. The two large trachae (*t t*) are pitted vessels. These may be surrounded by wood fibers and tracheids. The cambium is located at *c*. In the phloem (*ph*) are the seive tubes (*sv*) with their companion cells, and adjacent

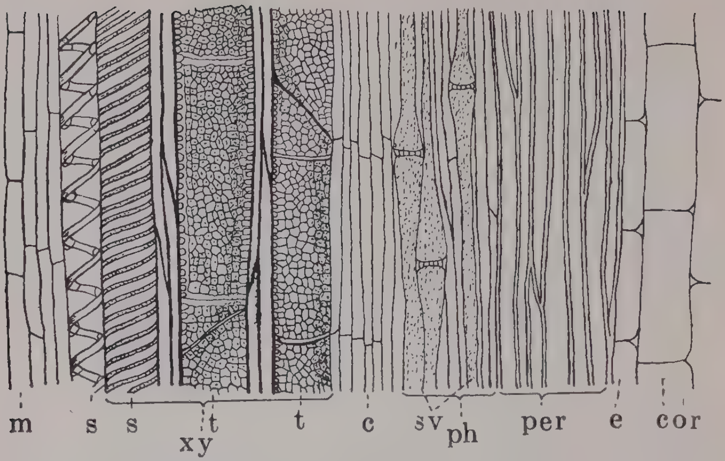

FIG. 22.—A radial longitudinal section of the vascular bundle of the sunflower simplified. *cor*, cortex; *e*, endodermis; *per*, pericycle; *ph*, phloem; *sv*, sieve tubes; *c*, cambium; *xy*, xylem; *t-t*, pitted vessels; *s-s*, spiral vessels of the protoxylem; *m*, pith. (Adapted from Vines.)

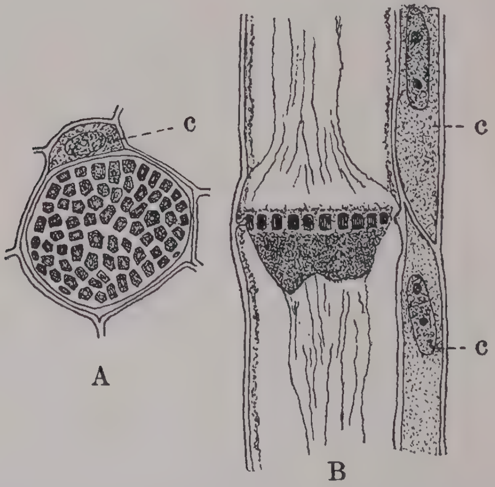

FIG. 23.—Portion of a sieve tube of the pumpkin (*Cucurbita pepo*). A, transverse sieve plate seen from the surface, and a companion cell, *c*. B, longitudinal section of a portion of a sieve tube with a sieve plate, and portions of two companion cells, *c*. (From Strasburger.)

parenchyma. The bast fibers of the pericycle are shown at *per*, the endodermis at *e*, followed by cells of the cortex, *cor*.

Portions of a sieve tube and companion cells in cross and longitudinal sections are shown in Fig. 23, A, B. The perforated cross wall is the sieve plate (A).

It will be observed that the elements of mature primary tissues are greatly elongated.

As stated, Fig. 22, represents a simplified vascular bundle. The xylem of the bundle may contain the following elements: *iracheal tubes* or vessels, *tracheids*, *wood fibers* and *wood parenchyma*. A tracheid is an elongated, thick-walled cell with more or less tapering ends. The diameter of the cell is usually greater than the thickness of the wall. There are spiral, annular, and pitted tracheids. An annular tracheid has its wall strengthened by ring-shaped thickenings on the inside. The spiral tracheid has spiral thickening. A pitted tracheid has a thick wall in which there are small rounded thin spaces or openings, the *pits*. A fiber is a narrow, elongated, thick-walled cell with very tapering or sharp pointed ends. The diameter of the cell cavity is usually no greater than the thickness of the cell wall. Fibers add strength to the stem. A tracheal tube or vessel is composed of a longitudinal row of two or more cells thrown into communication by the partial or complete absorption of the cross walls. There are annular, spiral, pitted, and reticulated vessels. The latter have reticulated or net-like thickenings.

Annular and spiral vessels occur in the protoxylem. They can be stretched and at the same time are kept open by the rings or spiral thickening.

Pitted or reticulated vessels are formed chiefly after the stem has elongated.

The phloem is composed of sieve tubes with their companion cells, bast fibers and phloem parenchyma.

A sieve tube consists of one or more cells which communicate with each other or with neighboring cells through very fine openings aggregated in circumscribed areas, the sieve plates. Sieve plates occur upon the longitudinal as well as upon the cross walls of the cells. Bast fibers are strengthening cells.

Collateral and Bicollateral Bundles.—When phloem and xylem lie side by side, the bundle is collateral. When phloem is present both on the outside and on the side next to the pith, the bundle is known as bicollateral. Bicollateral bundles occur in the stem of the pumpkin.

The structure of the stem composed of its adult or permanent primary tissues may be visualized in the diagramatic illustration of Fig. 24, which shows a part of cross and longitudinal sections.

Latex Vessels.—In the ground tissue of certain plants latex vessels occur which are tubes containing a milky fluid, *latex*, as in the common milkweed, lettuce, dandelion. Latex may be variously colored as in the Celandine Poppy (Stylophorum) and the Blood Root (Sanguinaria). Latex vessels are formed either from single cells or by the anastomoses of several cells.

The Course of Vascular Bundles in the Stem.—According to their course in the individual leafy stem, vascular bundles may be placed into two categories: (1) the cauline bundles, those that are confined exclusively to the stem, and that are formed acropetally as the stem grows; and (2) the common bundles, those which are common to both leaf and stem. Cauline bundles may or may not be connected with the bundles of the leaves. The bundle, or bundles, of the leaf that pass into the stem are known as *leaf trace bundles.* When followed from leaf into stem, they are found to pass down through two or more internodes and finally unite with other common bundles. Before uniting with other bundles they may or may not branch.

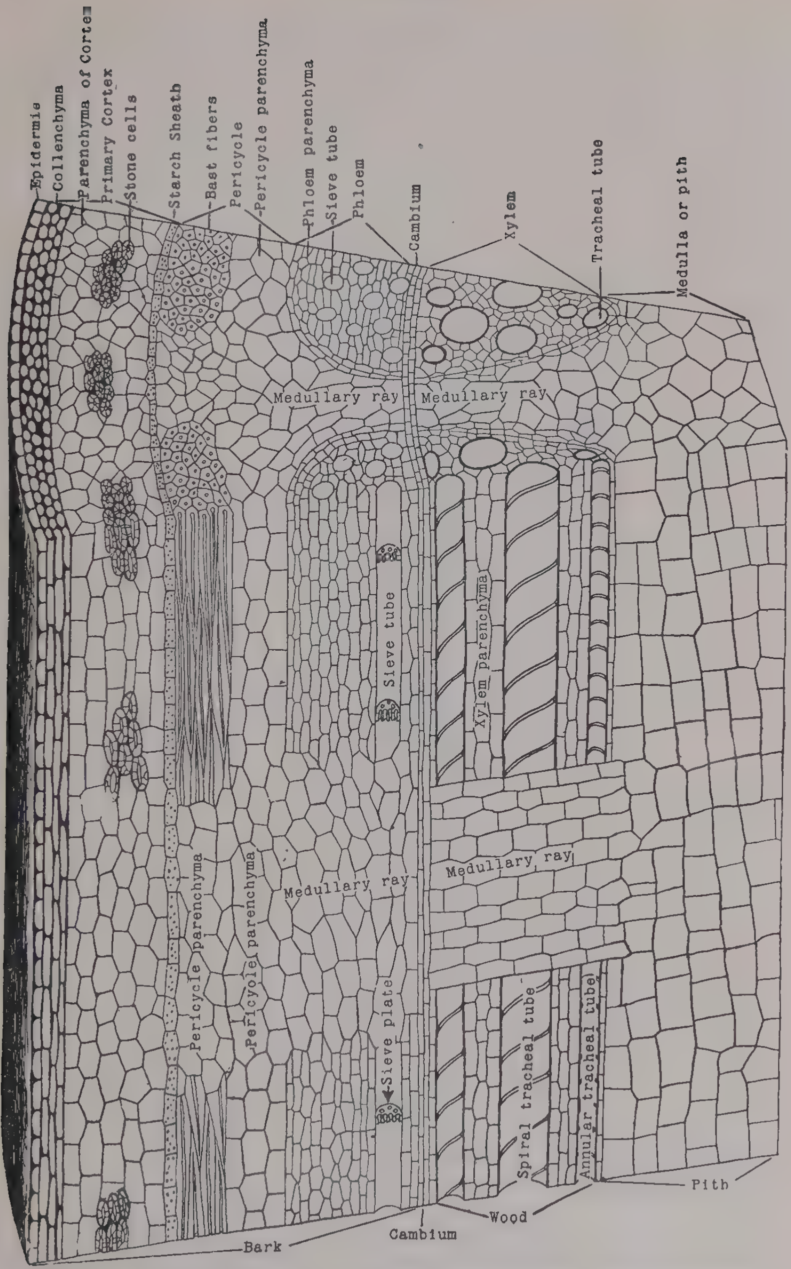

FIG. 24.—Diagram to show character and arrangement of tissues developed from primary meristems. Cambial activity has not yet begun. (From William C. Stevens' Plant Anatomy.)

In the dicotyledonous stem the leaf trace bundles usually pass down the stem at a definite distance from the surface. This accounts for the regular ring of bundles seen in a cross section of such a stem.

In monocotyoedonous stems the bundles of the leaves penetrate the stem to different depths, some reaching the center, before taking a downward course. For this reason the bundles are seen in a cross section of the stem to be distributed irregularly in the ground tissue.

The vascular bundles of the leaf of dicotyledonous plants, which usually form a network by anastomoses, generally unite into one or more larger leaf traces. The bundles of leaves and stems are always connected from the start with the bundles of the roots, and, because of this fact, the vascular tissue of the whole plant forms a unified conducting system, the system of rapid transit.

Secondary Thickening of Stems of Gymnosperms and Dicotyledonous Plants.—Stems that live but one season consist mainly of the adult primary tissues as described in the foregoing paragraphs, but in the oldest parts of the stem of old perennials, little of the mature primary tissue remains, perhaps some of the pith and the primary xylem. The bulk of such stems consists of tissues resulting from *secondary growth*.

Secondary tissues in such stems originate from two sources, the activity of the cambium and of the cork cambium. The cambium adds new wood and new bast each growing season or year, while cork is developed first in the cortex close beneath the epidermis and later in deeper layers of the cortex and even in the bast.

As illustrations of secondary thickening, we shall select the stem of a gymnosperm (Pinus) and one of an angiosperm, the linden (Tilia).

The Pine Stem and Its Secondary Growth in Thickness.—In the pine seedling the primary tissues are similar in arrangement and structure to those of an herbaceous stem of a dicotyledonous plant. In a two-year old stem, for example, we find in the center the pith which is primary ground tissue (Fig. 25, *p*). Surrounding this are two concentric rings of xylem, the annual rings, each the result of one season, or one year's activity of the cambium, (*ca*). The fine radiating lines are the rays (medullary rays). The primary rays extend quite to the pith; those that do not reach the pith are secondary rays. Continuing outwards beyond the cambium is the zone of phloem (*ph*), and following this is the primary cortex, in which are resin ducts. Many cells of the cortex contain chloroplasts.

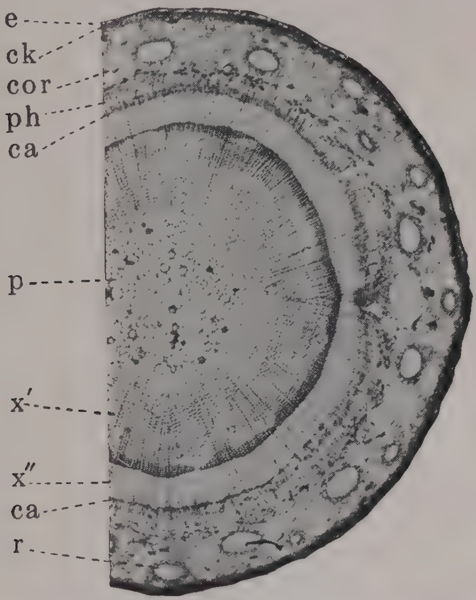

FIG. 25.—Portion of a cross section of a pine stem showing the first annual ring of wood and the spring wood of the second year. *e*, epidermis; *ck*, cork layer; *cor*, cortex, the large rounded openings being resin ducts (*r*); *ca*, cambium; *p*, pith; *x′* and *x″*, first and second annual rings.

The surface layer is the epidermis, the cells of which are now dead. Beneath the epidermis is the layer of cork to be mentioned in a subsequent paragraph.

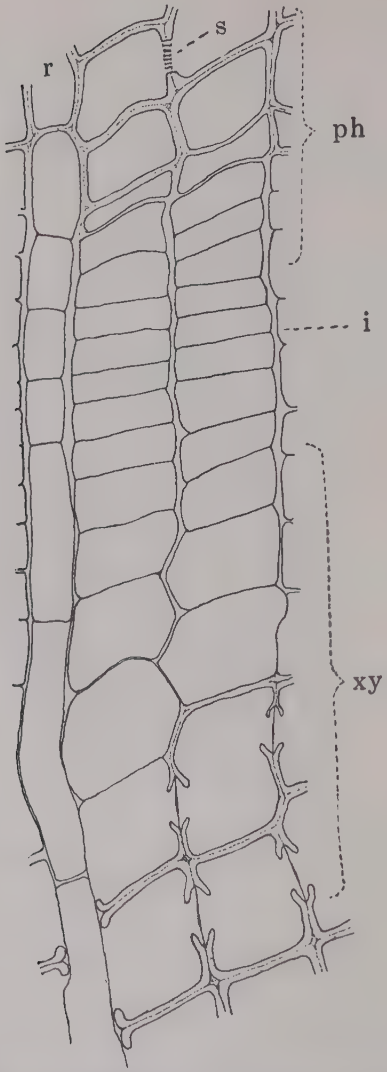

FIG. 26.—Portion of a cross section of the stem of *Pinus sylvestris*, showing young xylem cells, *xy*, and young phloem, *ph*, with cambium, *i*, between; *r*, ray; *s*, sieve area of sieve tube.

The Origin of Phloem and Xylem from the Cambium. As stated the cambium consists of a single layer of meristematic cells. Each cambium initial divides tangentially into two cells. One or both of these subsequently divide in the same plane (Fig. 26, *i*). In this manner radial rows of cells result. The cells next to the phloem mature into secondary phloem (*ph*), while those next to the xylem mature as secondary xylem (*xy*). A layer one cell in thickness (*i*) must remain as cambial initials. The cells of the phloem may remain meristematic for some time dividing in various directions. It is evident that the stem increases in girth by radial divisions of living cells.

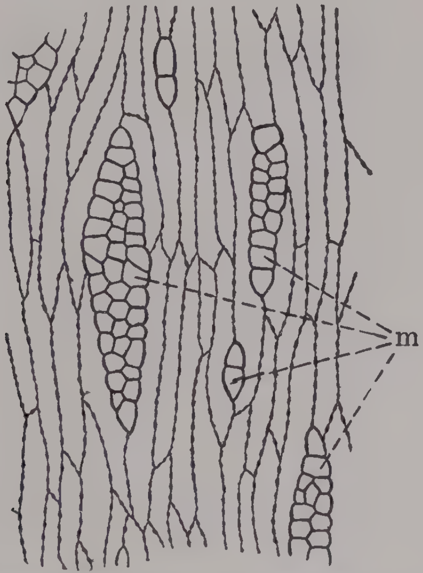

FIG. 27.—Tangential section through the cambium of the Elm, showing the elongated form of the cambium cells; *m*, groups of cambial cells forming medullary rays. (From F. O. Bower's "Botany of the Living Plant." By permission of the Macmillan & Company, Ltd., Publishers.)

In a longitudinal radial section the cambium cells appear long and narrow with square ends. If a longitudinal section be made in a tangential plane, the cambium cells will appear pointed and interlocked with one another (Fig. 27). The groups of cells at *m* in this figure are end views of young rays formed by the cambium.

The Mature Xylem of Pinus.—The bulk of pine wood consists of thick-walled cells arranged in radial rows. As will be seen from longitudinal sections, these cells are pitted tracheids, wood fibers and tracheal vessels being absent. Those tracheids formed during the earlier part of the period of growth are larger than those formed later. The large cells of the spring wood (Fig. 28, *s*) following abruptly the smaller elements of the latter part of the preceding season present a sharp line of demarcation. Consequently, each year's increment of xylem appears well defined as a ring.

The radial walls of the spring wood especially are marked by characteristic *bordered pits* (*bp*), appearing in cross section as two V's with the divergent limbs turned toward each other. Each bordered pit is a thin place in the cell wall, circular in outline, and with an overarching edge. In longitudinal radial views of the tracheid, the bordered pits appear as concentric circles. The inner circle represents the opening into the cell cavity, the outer circle being the outer limit of the pit next to the middle lamella. The thin partition with its centrally thickened part, the *torus*, is the primary layer of the cell wall, or closing membrane. The closing membrane permits liquids to pass from cell to cell, but inhibits the passage of bubbles of air, which tend to interfere with the movement of water through the tracheids. In a longitudinal radial section of the xylem the cells are seen to be elongated tracheids with interlocking, rounded or pointed ends (*c*). In longitudinal tangential section the bordered pits present the same appearance as in transverse section. The pits between the ray cells and tracheids are simple pits, and appear as single circles. In a tangential longitudinal section the rays are seen in end view.

The rays are thin strips of cells running in a radial direction. They are usually one cell in width but may be several cells in height, i.e., up and down in the stem. The upper and lower edges are flanked by pitted tracheids (*rt*). Resin ducts extend up and down in the wood. Those in the rays connect with the vertical ducts.

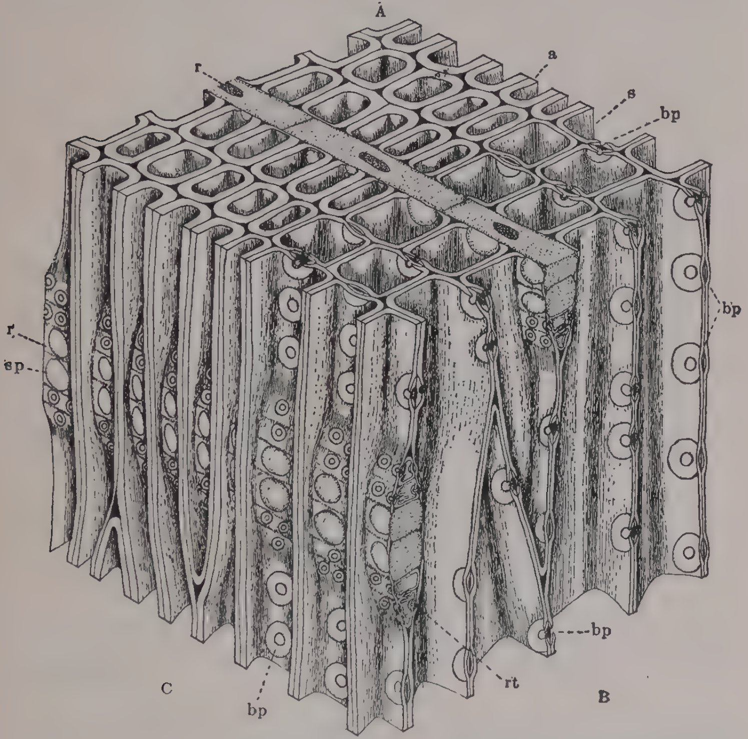

FIG. 28.—Perspective of a bit of pine wood including spring and summer wood. Upper face, A, cross section; B, tangential section; C, radial section. *r*, ray cells; *bp*, bordered pits; *sp*, simple pits; *rt*, ray tracheids; *a*, summer or autumn wood; *s*, spring wood.

Secondary Thickening of the Cortex.—As stated in a foregoing paragraph, a layer of cork develops beneath the epidermis, or in some stems in the epidermis. The layer or layers of cork constitute the secondary cortex.

The cork cambium, *phellogen*, arises either just beneath the epidermis or a few cells deeper. By tangential divisions a layer of cells is produced, those on the outside maturing as cork (Fig. 29). Corky walls are impervious to water, and the epidermal cells soon die.

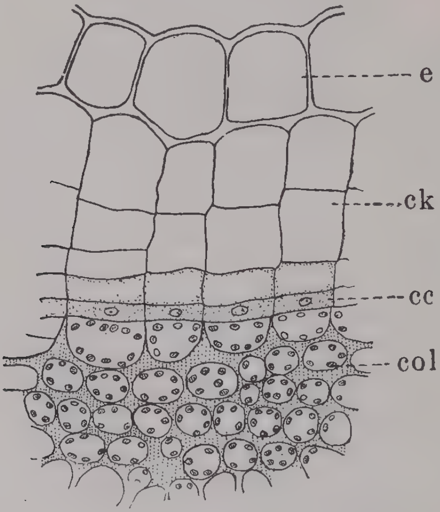

Fig. 29.—Section through the outer cortex of the stem of the elder (*Sambuscus canadensis*); *e*, epidermis; *ck*, cork layer; *cc*, cork cambium; *col*, thick-angled cells, collenchyma. (From Strasburger.)

The thick layer of cork of old tree trunks is produced in the following manner: After a time the first cork cambium dies, and a new cork cambium is developed deeper in the cortex. Later other cork cambiums are formed each deeper than its predecessor, and each in turn ceasing to function. Later new cork cambiums arise in the outer phloem. By the continued formation of new regions of cork cambium, and by the continued development of new phloem form year to year, a thick "bark" results.

As the stem increases in size from year to year the outermost layers of cork crack and break off as pieces of "bark." This is continued as long as the stem lives and grows.

Development of the Tall Smooth Trunks, or Boles, that Yield Fine, Clear Lumber.—As the pine tree ages, the lower branches gradually die and drop off. In thick or crowded stands of native or cultivated forests the trees become very tall comparatively early in life. Because of crowding or the lack of light, the death of branches proceeds more rapidly, and the result is a tall trunk free of limbs for a considerable height. The wood formed by secondary thickening after the branches fall is free from knots. It yields clear lumber. A knot is the cross section of a branch. The remains of the limbs which have dropped off appear as "dry knots" in sawed lumber. If the branch remain alive on the tree, the secondary wood grows around it, and a "live knot" is the result.

Stem of Perennial Dicotyledonous Plants.—Stems of annual plants, such as those of corn and sweet clover, last but one year or season. Those of perennial plants, such as woody bushes and trees, persist from year to year becoming larger with age. The aerial stems of broad-leaved perennials change both in external appearance and in internal structure from the annual type.

At the beginning of the colder seasons in temperate regions, the leaves mature and fall from the plant. The structures which were formed during the growing season, and which contain much of the next season's growth, now appear as scaly or fleshy buds, the winter buds, occupying terminal and lateral positions on the shoot (Fig. 30, *tb*, *ab*). The places at which the fallen leaves were attached to the stem are conspicuously marked by scars, the *leaf scars.*

In many woody perennial stems, near the close of the first season's growth, the epidermis dies, and beneath it there is developed a layer of cork, as already described, which imparts the darker color to the surface of the stem and conceals the green tissue of the bark beneath. In plants whose branches remain green, the epidermis lives longer, and the corky layer is slow in developing, or does not develop at all. Scattered over the surface of the stem are many small pustule-like protuberances, the *lenticels* (Fig. 30, *l*).

Lenticels.—Lenticels are openings in the cork layer, which form a communication between the air and the live cells beneath. In other words they are ventilators in the cork. They are formed as follows. Beneath certain stomata the cork cambium, instead of producing a layer of cork, will give rise to a mass of thin-walled cells with intercellular spaces. By an increase in size these masses finally break through the epidermis and project beyond the surface of the stem. Cork is water-proofing material. This property is due to a substance, suberin, deposited in the walls, which is impervious to water. A demonstration of this property may be seen in the tuber of the white or Irish potato. Potatoes unpeeled will remain fresh for days and even months in a moderately dry atmosphere. The rapidity, however, with which a peeled potato will dry out and become hard is a

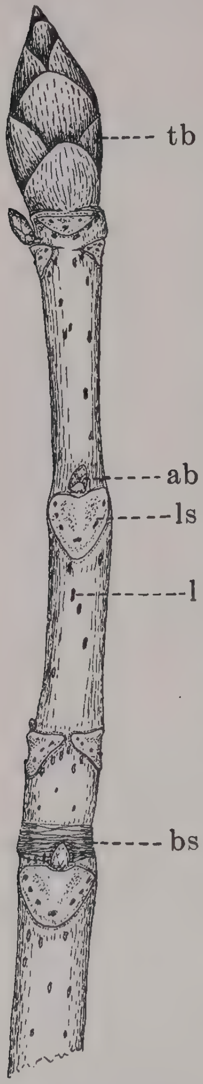

Fig. 30.—End of a branch of the horse chestnut (*Aesculus hippocastanum*) in the winter condition. *tb*, terminal bud; *ab*, axillary bud. *ls*, leaf scar; *l*, lenticel; *bs*, scars of bud scales of terminal bud of previous year.

familiar phenomenon. Peeling "new" potatoes consists in removing the thin "skin" which is composed of the epidermis and the layer of cork beneath.

The cork of most woody plants is not suitable for commercial purposes. Commercial cork used in making bottle stoppers, etc., is derived chiefly from species of oak native to Spain and southern France.

The protecting character of cork is indicated by its physical properties. Besides being impervious to water, it is a poor conductor of heat and electricity; it is not readily corroded by acids and alkalies; it does not decay rapidly, and it is not so likely to be eaten by insects and small animals as are many other parts of the plant.

Cell walls containing suberin turn yellow under a proper application of chlor-zinc iodine, or sulphuric acid and iodine.

Fall of Leaves.—In the autumn the leaves of our deciduous trees mature and fall from the plant. This is a normal process. As the leaf matures, there is formed beneath the leaf base a layer of cork, which affords protection to the cells of the cortex beneath. In the meantime a layer of specially developed cells is formed between the outer part of this cork and the base of the leaf. These cells, which remain tender and thin-walled, constitute the *cut-off*, or *absciss layer*, permitting the leaf to fall of its own weight (Fig. 31). After a frosty night, especially following a rain, the leaves drop readily and in profusion on the following morning. The water taken up by the cells between the cork layer and the leaf base freezes, and the resulting expansion severs the connection so that the leaf drops as soon as the ice melts. Scattered over the surface of the leaf scar are to be seen the dried ends of the vascular bundles that passed from the leaf to the stem. The bundles were largely pinched in two by the formation of the cork and absciss layer.

There are, however, many exceptions to the method of leaf fall just described as it is not common to all plants. In many cases there is no separating layer developed. The leaves die, dry up, and remain attached to the twigs for a longer time, or during the winter, falling only when the buds begin to expand in the following spring. Examples are to be found among the beeches and oaks.

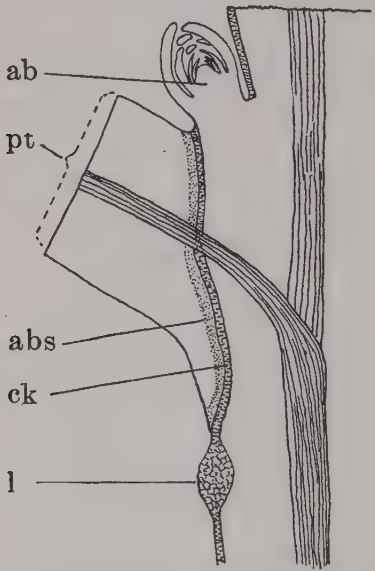

FIG. 31.—Longitudinal radial section through the base of a leaf and a portion of the stem of the Horse-chestnut (*Aesculus hippocastanum*) to which it is attached. *pt*, petiole; *abs*, absciss layer; *ck*, cork; *l*, lenticel; *ab*, axillary bud. (Adapted from F. O. Bower's "Botany of the Living Plant." By permission of the Macmillan & Company, Ltd., Publishers.)

Buds.—As already stated a bud consists of the growing point of a stem more or less completely covered by some sort of leaves. In scaly buds, such as the winter buds of woody plants, the tender parts within are protected by over-lapping scale leaves (Fig. 32).

Bud scales are modified leaves, whose chief function is to protect the more tender members within from desiccation during the months of dormancy, freezing and thawing being a drying process. Naked buds are not protected by scales, the outer parts consisting of young foliage or other leaves. They are found on some woody plants and on almost all herbaceous plants. A longitudinal section of a scaly bud containing young foliage leaves only is shown in Fig. 32. The young leaves are often covered with numerous hairs. The bud scales may also be provided with a covering of hairs or waxy secretions.

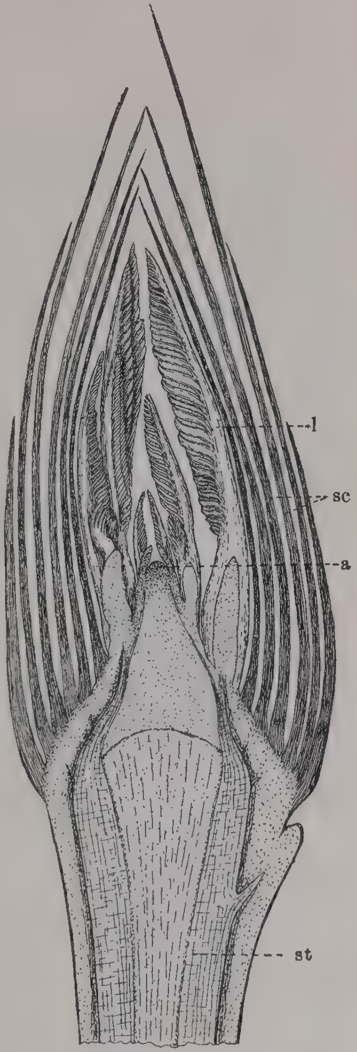

FIG. 32.—Longitudinal section through a terminal bud of the Shellbark Hickory (*Hicoria ovata* (Mill.) Britton). *st*, stem; *a*, growing point; *l*, young foliage leaves; *sc*, bud scales.

Classification of Buds.—Buds may be classified, (1) as to the characteristic structures contained, (2) as to their position on the stem, (3) and as to their time of development.

As to structure of internal parts, buds are known as *leaf*, *flower*, and *mixed* buds. A leaf bud contains young leaves only. A flower bud contains one or more unopened flowers. A mixed bud contains both flowers and leaves.

As to position buds are *terminal*, *axillary*, *accessory* or supernumerary, *sub-petiolar*, and *adventitious*.

The bud that ends a main stem or branch is a terminal bud. Axillary buds arise in the axils of the leaves. Accessory buds arise above and sometimes a little to one side of the axils. Sub-petiolar buds as in the sycamore, develop beneath the base of the leaf. They are usually not visible until the leaf falls.

Adventitious buds arise any where out of the ordinary positions just mentioned.

Latent buds are those that remain undeveloped. They may become overgrown by successive layers of woody tissue where they may remain permanently, or until something in the life of the plant enables them to become active and grow to the surface.

Internal Structure of a Perennial Dicotyledonous Stem. Cross Section.—As an illustration we shall use a cross section of a three or four year old twig of the Linden. Three well defined regions are readily recognized: the central pith, the wood, and the bark. Between wood and bark is the cambium (Fig. 33). The wood, as in the pine, is disposed in well defined concentric annual rings, each ring representing usually a year's growth. The rings may vary considerably in width, and any ring may be wider on one side than on the side directly opposite. In the spring, as soon as the leaves have fully expanded, a large volume of water passes up through the stem. The larger volume of water requires larger vessels for its transportation, and the bulk of the water passes through the young wood.

The lines running radially through the xylem are the *vascular rays*. Those that extend from the pith quite into the bark are the *primary rays*, while those that do not extend to the pith are the *secondary rays*. The primary rays are usually two cells wide in a transverse direction, occasionally wider; the secondary rays are one cell wide. In a vertical direction,—up and down the stem,—the rays may be several cells in height.

In detail the xylem consists of large pitted ducts, pitted tracheids, and those strengthened by spiral thickenings, wood fibers, and wood parenchyma. The vessels, or ducts, tracheids, and woody fibers are without protoplasmic contents. The wood parenchyma cells contain protoplasm, and usually much starch. The wood fibers are mainly to enhance the mechanical stability of the wood.

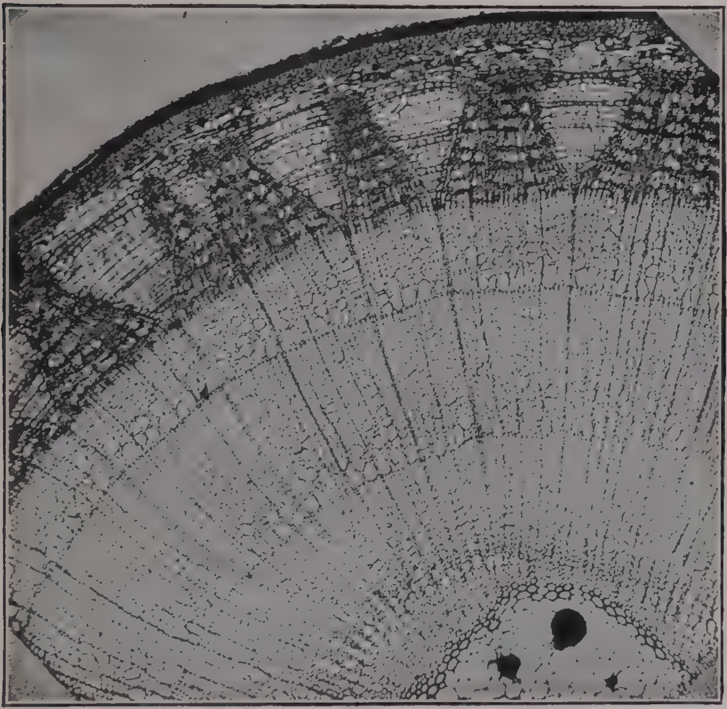

FIG. 33.—Linden (Tilia). Cross section of a three year old stem. Note the funnel-shaped widening of the outer ends of the primary rays and the wedge-shaped masses of phloem. (From Gager's "General Botany." P. Blakiston's Son & Company.)

The activity of the cambium is the same as described in Pinus. The masses of bast are somewhat keel-shaped, being narrower toward the outside (Fig. 33). These masses reveal alternating bright and dark layers running tangentially. The light, or shiny, layers are composed of very thick-walled bast fibers. The dark layers are composed of smaller cells containing starch, the bast parenchyma, and larger cells, the sieve tubes, with their companion cells. The number of bands of bast fibers is about twice that of the annual rings. It is readily seen also that the primary rays widen out funnel-wise at their outer ends, separating two keel-shaped masses of bast (Fig. 33).

The chlorenchyma of the primary cortex forms a complete encircling zone. In many cells of the cortex, and of the outer parts of the rays, are large crystals of calcium oxalate. More externally is a layer of collenchyma cells, containing chlorophyll, and whose cell walls are glistening white in unstained sections, and especially thick at the angles. Finally the outermost part of the bark consists of the primary layer of cork, and lastly the epidermis. The epidermal cells are dead, and owing to the enlargement of the stem, are broken here and there. The primary layer of cork is several cells in thickness.

As the stem increases in diameter from year to year, the outermost layer or layers of corky tissue crack and break off as pieces of bark as in the Pine. This process continues as long as the tree grows. The manner in which the bark splits and breaks off is often characteristic of the species. In the birch, for example, the bark breaks off in very soft, thin layers, or in the shag-bark hickory as long, saber-like strips.

Heartwood and Sapwood.—In a cross section of an older tree trunk, such as the red mulberry, common black locust, oak, etc., we see that the woody cylinder consists of a light-colored outer zone, the sapwood, *alburnum*, and a darker central zone, the heartwood, or *duramen.* The line of demarcation between the two is usually sharp and regular. In the sapwood many of the wood parenchyma cells are alive, while the heart wood is composed wholly of dead cells, those from which the living contents have disappeared. The outer layers of the sapwood especially are saturated with water, and it is through the sap wood that water ascends in the tree trunk.

Sapwood is changed into heartwood by the deposition in the cell walls and cell cavities of various substances such as resins, gums, tannin, mineral elements, and pigments. These substances give to the heartwood its color and durability, and at the same time render it unfit as water conducting tissue. The vessels of the heartwood in many trees are plugged by parenchyma cells, *tyloses,* which develop from growths of adjacent wood parenchyma cells, which penetrate the thin places in the walls of those vessels. Tyloses are present in such trees as the black locust (*Robinia pseudacacia*) and the white oak (*Quercus alba*).

The pigments impart the characteristic colors to the various woods. Woods which are durable in contact with the soil owe their durability to the substances mentioned above. Those substances prevent in a large measure the growth of the wood destroying fungi.

Black locust and white oak wood have been found to be sound after standing longer than forty years as fence posts.

Structure of a Monocotyledonous Stem.—As an illustration of the structure of a monocotyledonous stem, we shall select that of Indian corn (*Zea mays*).

In a cross section of a young internode one recognizes readily the numerous vascular bundles somewhat evenly spaced in the pith-like ground tissue, but not arranged in any definite order (Fig. 34). Near the periphery the bundles are smaller and more numerous.

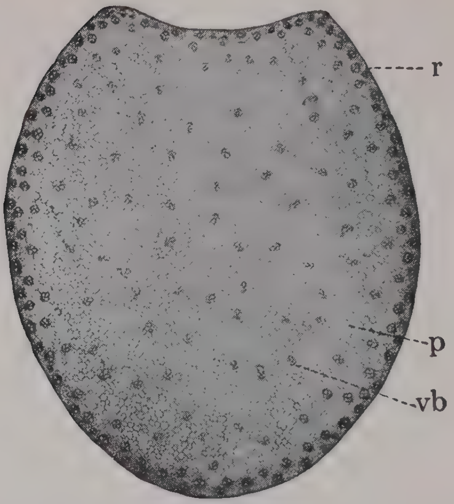

FIG. 34.—Photomicrograph of a cross section of an internode of the stem of corn (*Zea Mays*). *r*, rind; *vb*, vascular bundles; *p*, pith, or ground tissue.

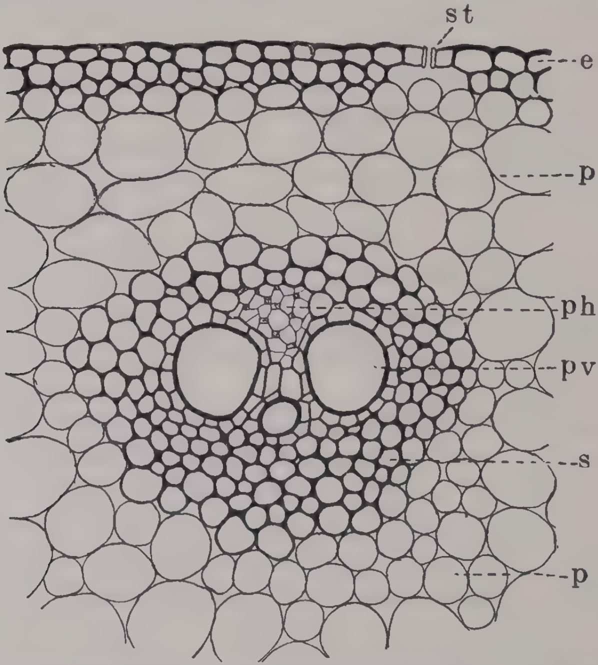

FIG. 35.—Portion of a cross section of the periphery of a young internode of Corn. *st*, stoma; *e*, epidermis; *p*, parenchuma; *ph*, phloem; *pv*, pitted vessel; *s*, sclerenchyma.

On the outside is the epidermis consisting of a row of small cells of uniform size. Beneath the epidermis is a zone of sclerenchyma cells in which are spaced the numerous smaller vascular bundles (Fig. 35).

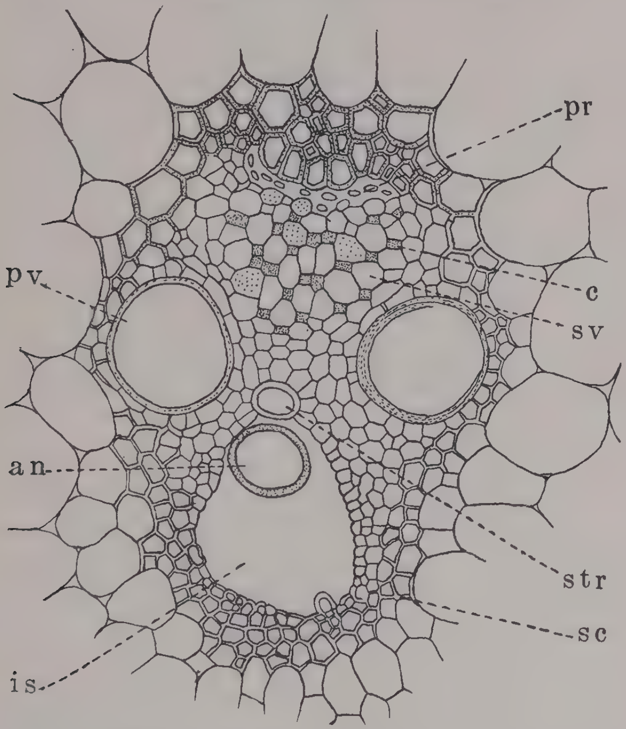

Fig. 36.—Cross section of a vascular bundle of an internode of the stem of corn (*Zea Mays*). *an*, ring of an annular vessel; *pv*, pitted vessel; *str*, spiral vessel; *is*, intercellular space; *pr*, protophloem; *sv*, sieve tube; *c*, companion cell; *sc*, schlerenchyma sheath.

This zone develops into the hard rind of the corn stalk. The soft pithy tissue composing the larger and central part of the stem is composed of thin-walled parenchyma cells with intercellular spaces.

The Vascular Bundle.—In the vascular bundle, the phloem and xylem lie side by side, the phloem facing the periphery of the stem (Fig. 36). At the outer edge of the phloem is a narrow band of crushed cells, the *protophloem* (*pr*). The rest of the phloem is composed of larger cells somewhat hexagonal in outline with small square cells distributed among them. The larger (*sv*) are the sieve tubes, and the smaller, the companion cells (*c*).

In the xylem are generally present two large and conspicuous pitted vessels (*pv*). At the inner angle of the xylem region may be a large intercellular space (*is*). Bordering upon the intercellular space are two vessels, an annular (*an*) and a spiral vessel (*str*). These make up the protoxylem. Surrounding the entire bundle is a band of thick-walled cells, the *sclerenchyma sheath*.

The large intercellular space (*is*) is formed by the breaking down of cells, while the intercellular spaces between the cells of the pith are produced by the separation of these cells at the corners.

Increase in Diameter of the Corn Stem.—With few exceptions stems of monocotyledonous plants do not increase in thickness by means of secondary tissue. There is no cambium between phloem and xylem of the vascular bundles of monocotyledonous plants save in exceptional cases, one of which is the common Yucca.

The increase in thickness is accomplished by the multiplication of the cells of the ground meristem. The manner in which this is accomplished may be illustrated in the growth of the corn stalk. The stem of the seedling, consisting of a few nodes, scarcely exceeds three or four millimeters in diameter while that of the thickest part of the mature stem may be as large as one's wrist.

These first few nodes and internodes do not thicken appreciably with age, but those developed subsequently become thicker until the maximum diameter is reached (Fig. 37). When any growing internode has attained its maximum diameter it does not become any thicker with age.

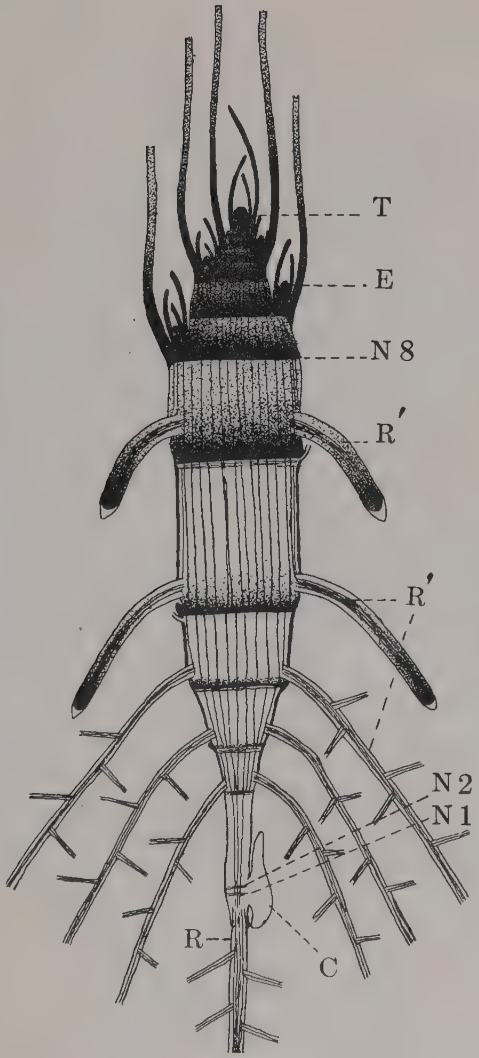

FIG. 37.—Diagram of a longitudinal section of a young corn plant. Meristematic regions are shaded black. *c*, cotyledon; *r*, primary root; *r′*, *r′*, adventitious roots; n'-n^8, nodes; *t*, growing point; *e*, bud.

The increase in size results from the multiplication of ground tissue cells in the meristematic regions back of the primordial meristem. Meristematic tissue persists for some time at the base of each internode, and it is from these regions that secondary roots develop.

As meristematic development ceases at the growing end of the stem with the formation of the tassel, the terminal internodes, those above the ear, elongate rapidly with but relatively little increase in thickness.

The Fern Stem.—The stem of our ordinary ferns (Polypodiaceae) is usually a branched rhizome growing horizontally upon the soil or a few inches beneath its surface. Leaves tend to spring from the upper side and roots from the lower. The growing point is not protected by scale leaves but by the young foliage leaves and numerous brown hairs and scales or only by the latter. The primordial meristem consists of a large apical cell from which the protoderm, the ground meristem and the procambial strand or strands are derived. There are no axillary buds. In unbranched stems the apical cell is the continuation of that originating in the stem quadrant of the embryo. Secondary tissues are not developed in the fern, consequently the mature parts of the plant consist only of the permanent primary tissues.

In the mature stem of *Adiantum pedatum* or *Dicksonia punctilobula*, the type used as our illustration, the procambium arises as a cylindrical zone enclosing the pith. This zone differentiates into a central xylem completely surrounded by the phloem (Fig. 38). The endodermis forms a complete boundary between ground tissue and the vascular cylinder both externally and on the side of the pith.

From the young procambial cylinder strands pass off into the leaves. Just above the insertion of each leaf-strand a small area does not differentiate into vascular tissue but consists of ground tissue, which connects the pith with the peripheral ground tissue. The vascular cylinder appears thus to be perforated by the ground tissue.

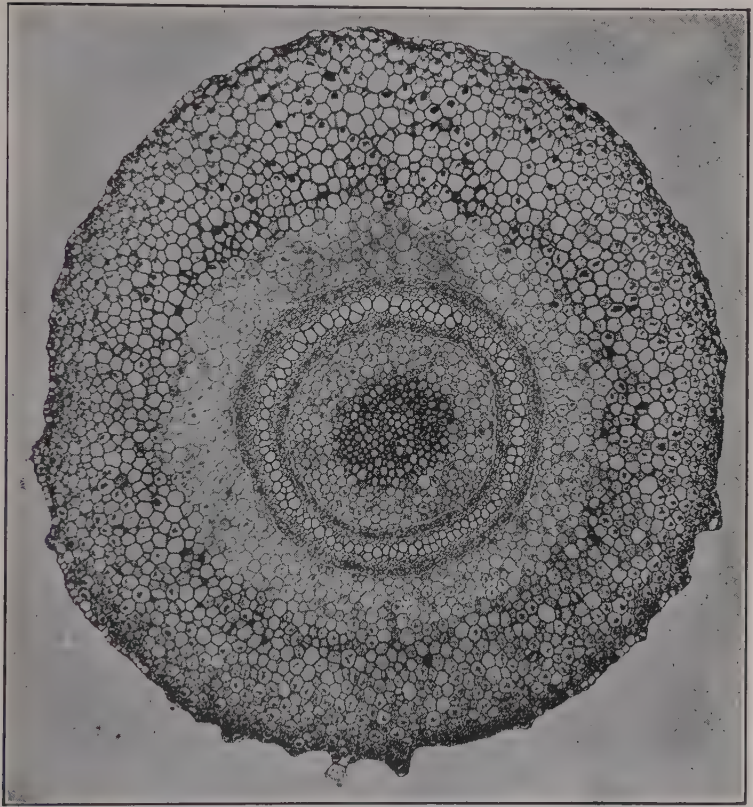

FIG. 38.—Cross section of the stem of *Dicksonia punctilobula*. Beginning at the outside the tissues are as follows: the epidermis, the cortex, and the vascular cylinder (siphonostile) enclosing the pith; in the vascular cylinder the outer phloem, the xylem and the inner phloem; the endodermis which surrounds the cylinder on the outer and inner sides belongs to the ground tissue. (From Chamberlain "Methods in Plant Histology.")

The space occupied by the connecting ground tissue is a *foliar gap*. The vascular tissue of the stem consists, therefore, of a perforated cylinder, a perforation, or foliar gap, being present at the insertion of each leaf trace (Fig. 39).

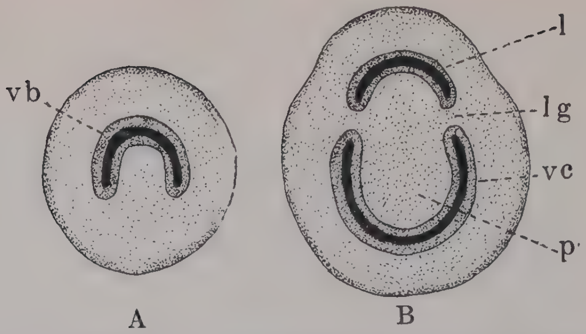

FIG. 39.—Diagrams of a cross section of the stem and of a leaf stalk of Adiantum. A, leaf stalk; *vb*, vascular bundle. B, stem, showing leaf trace, *l*, foliar gap, *lg*; *vc*, vascular cylinder; *p*, pith; xylem, solid black; phloem, stippled.

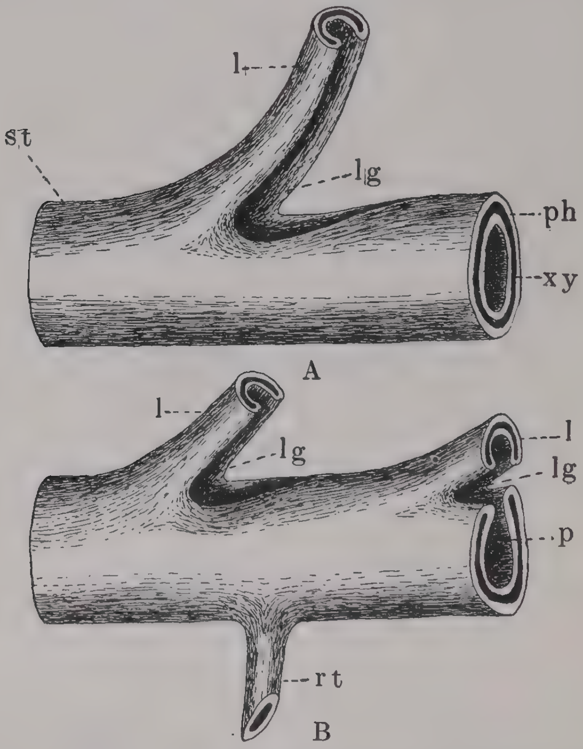

FIG. 40.—Perspectives of portions of the vascular system of Adiantum (cortex and pith not included). A, showing a leaf trace, *l*, and a leaf gap, *lg*. B, two leaf traces, two leaf gaps, and a root, *rt*.

If the section be made to pass through the stem at the base of a leaf, the vascular tissue will appear as two crescents with their openings facing each other, while in the leaf stalk a single crescent will be seen in the form of a horse-shoe (Fig. 39, A, B). Fig. 40 which represents portions of the vascular cylinder only, the ground tissue being omitted, will greatly aid in visualizing the form of the vascular system.

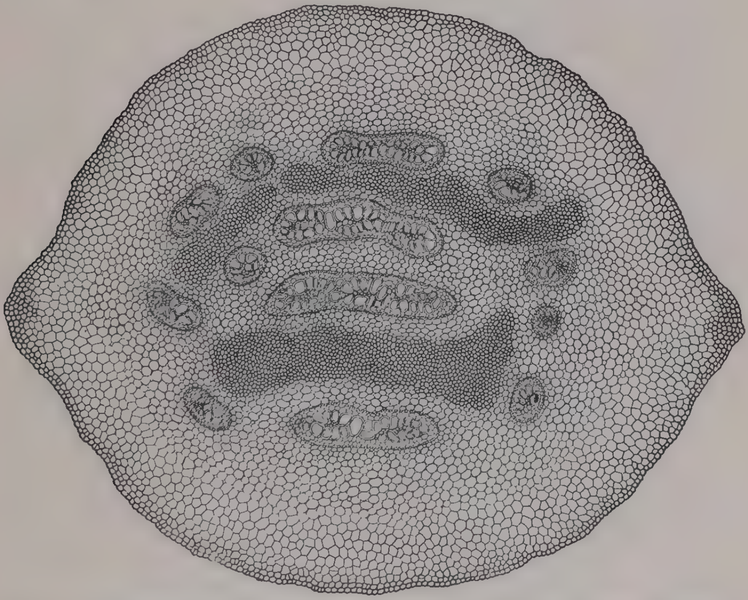

Fig. 41.—Cross section of the stem of the Brake Fern (*Pteris aquilina*). Explanation in text.

A cross section of the stem just below the base of the leaf will show the ring-shaped zone of vascular tissue with pith enclosed, and surrounded by the peripheral ground tissue (Fig. 38).

In the type of stem illustrated by the brake fern (*Pteris aquilina*) separate procambial strands are formed in the adult stem just back of the growing point. The main strands, which are connected by short branches, send off leaf traces to the leaves. The result is a vascular net work instead of a perforated cylinder. A cross section of the stem of Pteris is shown in Fig. 41, in which are seen the several vascular bundles.

The peripheral ground tissue of the fern stem consists largely of golden-brown thick walled cells. Stony cells may occur also in the pith region. In the bracken stem two bands of stony tissue run lengthwise near the center of the stem, between which are the two main vascular strands (Fig. 41).

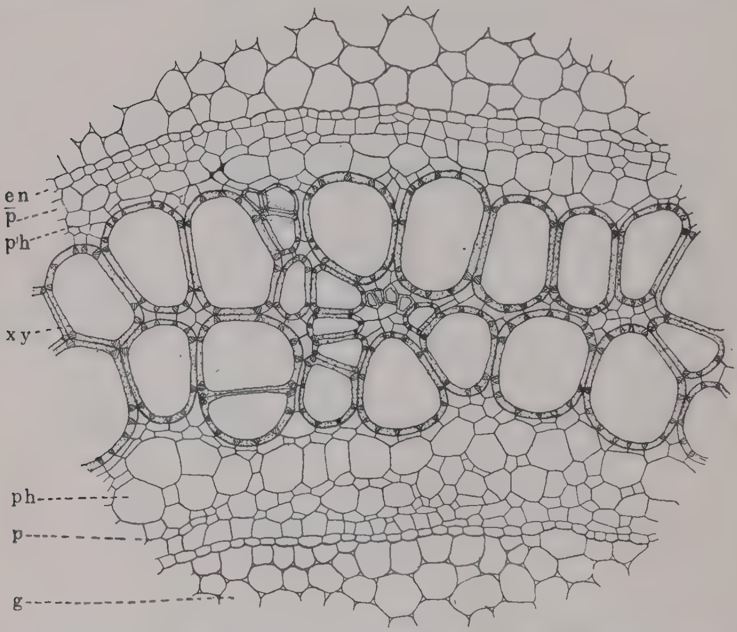

FIG. 42.—Cross section of a portion of a vascular bundle of *Pteris aquilina*. *en*, endodermis; *p*, pericycle; *ph*, phloem; *xy*, xylem; *g*, ground tissue.

Turning our attention now to the detailed structure of the vascular tissue, we see, in cross section, that it is immediately surrounded by a clearly defined row of cells, the *endodermis*, or *bundle sheath* (Fig. 42, *en*). The central part is composed of large, thick-walled cells, the *xylem* (*xy*), which is surrounded by the phloem (*ph*). The phloem consists of thin-walled cells, many of the larger being sieve tubes. One or two rows of cells just within the endodermis make up the *pericyle* (*p*).

The xylem appears as thick-walled cells closely pressed together. The conspicuous line separating the cells is the *middle lamella.* As will be seen in a longitudinal section, the xylem is made up largely of elongated tracheids with numerous transverse pits arranged like the rungs of a ladder (Fig. 43). For this reason these elements are called *scalariform tracheids.* The xylem first developed in the bundle (protoxylem) consists of smaller tracheids with spiral or reticulate thickenings. The longitudinal walls of the sieve tubes are marked by numerous sieve areas (Fig. 43, B). Within the various parts of the ground tissue are often developed strands of dark brown sclerenchymatous cells (stony tissue), which give to the stem a certain rigidity. These cells have very thick, striated and pitted walls.

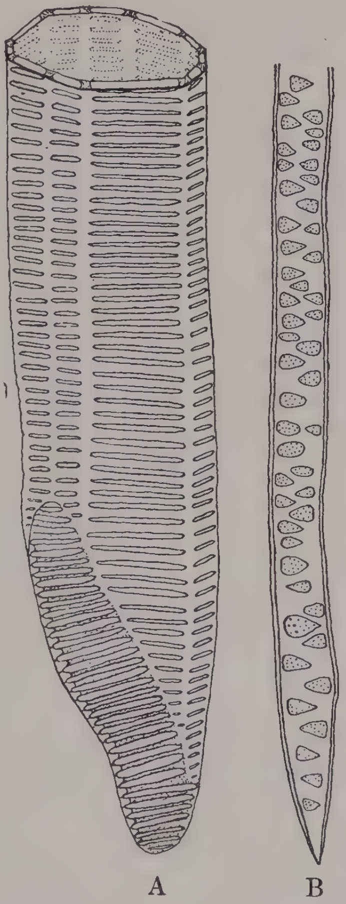

Fig. 43.—A, portion of a scalariform tracheid of Pteris. B, portion of sieve tube showing numerous sieve plates.

Kinds of Stems.—In presenting stem structure in the foregoing paragraphs we have selected those which may be regarded as typical of the majority of plants. Differing from the ordinary type are very many which owe their differences to duration, habitat, and special functions.

As to duration stems, as well as whole plants of which they are a part, are known as *annual*, *biennial*, and *perennial*. An annual is one that dies at the end of one year or growing season. An annual plant completes its entire life cycle within a year. Biennials are those which require two years to complete a life cycle. Examples are the mullen, hollyhock, teasel, etc. Perennials live several to many years. After attaining reproductive maturity they may produce seeds or only spores annually.

Herbaceous stems are those which do not become woody. The aerial branches of herbaceous perennials may die down each year.

The structure and habit of the stem depend also upon whether it grows above or under the ground. Those which maintain an upright position in the air without support from some other source are mechanically strong like a pillar or column, as is the case with large trees; others combine certain rigidity with great flexibility, as in the cereals. Wheat and rye sustain a very heavy load at the tip of the stem. In proportion to their height and diameter such stems combine unusual strength with great flexibility.

Stems like that of the pumpkin, grape vine, and the great lianas of the tropics, have very long slender stems, which can not maintain an upright position in themselves. They must either trail upon the ground or clamber or twine upon or around some other support.

Anatomically these stems are strong, but their tissues are differentiated in such a manner as to impart strength like that of a cord or cable.

Stems that cling to flat surfaces, or clamber over other plants or other objects are maintained in that position by special organs of support, which are modified leaves, branches or roots. Twining stems wind about a slender support, as seen in pole beans, morning glories, and the hop vine. Some like the hop twine clockwise; others counter clockwise.

Stems and branches that live under ground or partly covered by the soil are classified as rhizomes, bulbs, corms, and tubers.

A *rhizome*, or rootstock, is generally a thick fleshy stem, bearing scale leaves at the nodes, and which sends up aerial branches. Examples are the May Apple, Solomon's Seal, Iris, and the stems of many ferns. The rhizome is especially a food storage organ.

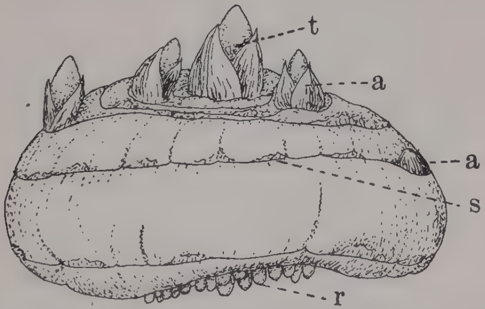

FIG. 44.—Corm of Gladiolus. *t*, terminal bud; *a*, axillary buds; *s*, leaf scar; *r*, roots.

A *bulb*, such as occurs in the onion, tulip and hyacinth, consists of a short flat or conical stem bearing thick overlapping, fleshy scales. Buds may arise in the axils of these scales. Bulblets or bulbils are little bulbs. The term *bulbil* is applied to the small fleshy bulbs produced upon the aerial stems of the tiger lily. Top sets of the onion are bulblets.

A *corm* is found in the Crocus, Gladiolus, Indian Turnip, etc. It is a short, solid stem covered by thin, membraneous leaf bases. Buds may arise in the axils of these leaves, and, as in other plants, corms bear terminal buds (Fig. 44).

A *tuber* is a thick fleshy stem growing above or under ground bearing scale leaves and axillary buds called "eyes." The white or Irish potato is an example. The scale leaves may be observed upon a very young potato. Bulbs, corms, and tubers are food storage organs, and also organs of vegetative propagation.

A *stolon,* or runner, is a slender stem creeping upon the surface of the ground, but frequently in the soil. A well known runner is that of the strawberry vine. Stolons may develop roots and buds at the nodes. Stolons often effect rapid vegetative propagation. As such they are produced by a wide range of plants from ferns to the Spermatophyta. The slender under-ground branch of the Irish potato plant whose tip develops into the tuber is a stolon.

Stem tendrils are twining or clasping organs of support, such as occur in the grape vine and Virginia Creeper. Their structure and origin distinguish them from leaf tendrils.

A *thorn* is a sharp pointed stem, either branched or unbranched. Young thorns bear leaves, a fact by which their stem nature is easily recognized.

Cladodia are green stems which perform the function of foliage leaves. The leaves borne by such stems exist in some modified form, such as scales or spines. Various Cacti and the garden Asparagus are illustrations. The fine soft needlelike spray of the Asparagus are not leaves but stems.

CHAPTER IV

THE ROOT

The ordinary roots of all groups of vascular plants that grow in the soil are strikingly similar in appearance; and their structure is relatively uniform throughout, being less complex, as a rule, than that of the stems.

The Growing Point of the Root.—The growing point of roots is covered by the root cap which affords protection for the tender parts beneath. The relation of the root cap and the rounded end which it covers is seen in a median longitudinal section (Fig. 45). In many roots a sharp boundary line is visible between the growing point proper and the root cap. The meristem (*cgn*) from which the cells of the root cap are replenished lies at the base of the cap just outside the line of demarcation. In some roots as that of the pea (Pisum) there is no sharp boundary between root cap and the tissue back of it. The oldest cells of the cap are injured and destroyed as the result of injury in the soil caused partly by the pressure of the elongating root; or they may slough off normally.

The primordial tissue of the rounded growing end is confined to a small region at the extreme tip, not exceeding two or three layers of cells in thickness. This region gives rise to the protoderm (*d*), the cortex or *periblem* (*pbm*), and the procambial cylinder, *plerome* (*pl*). The *endodermis* (*en*) is derived generally from the cortex.

Back of the meristematic tissue is the region of elongation and still farther back is the region of maturation or internal development. Root hairs are developed from the epidermis. These begin in the region of elongation and reach their full development a short distance in the maturing region. In older parts of the root, the root hairs die and disappear. Root hairs live a comparatively short time, however as the old die new

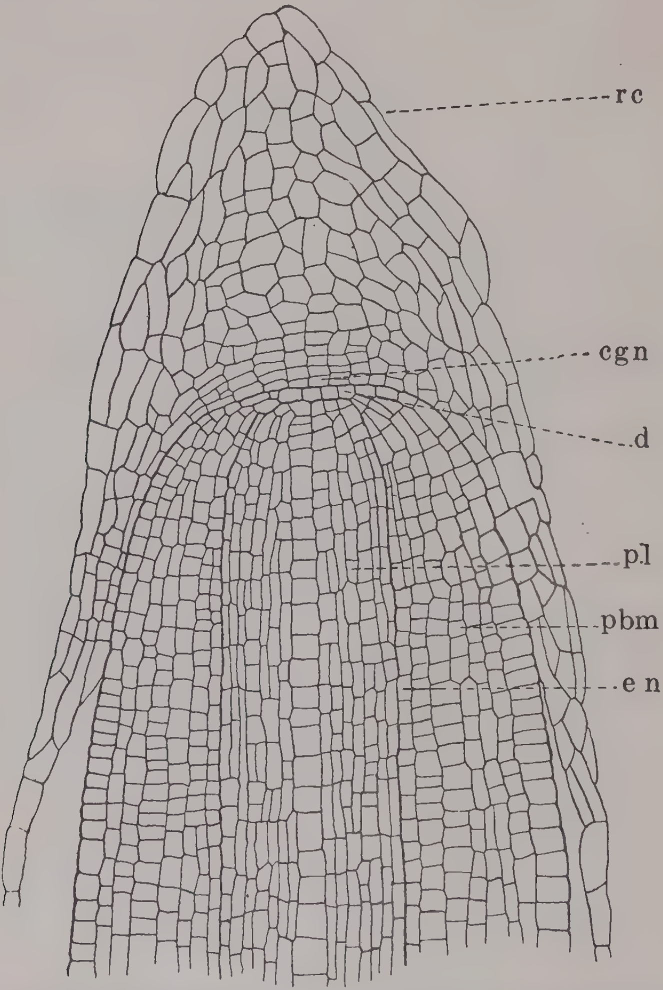

Fig. 45.—Longitudinal section through the root tip of Tradescantia. *rc*, root cap; *cgn*, calyptrogen or meristem producting the root cap; *d*, protoderm; *pbm*, periblem or cortex; *en*, endodermis; *pl*, procambial strand or plerome.

hairs are constantly being produced towards the tip. With progressive growth of roots, the absorbing surface is brought constantly into new regions from which water and mineral elements are secured.

In some trees the root hairs are multicellular and they may remain functional for a longer time than in the majority of plants.

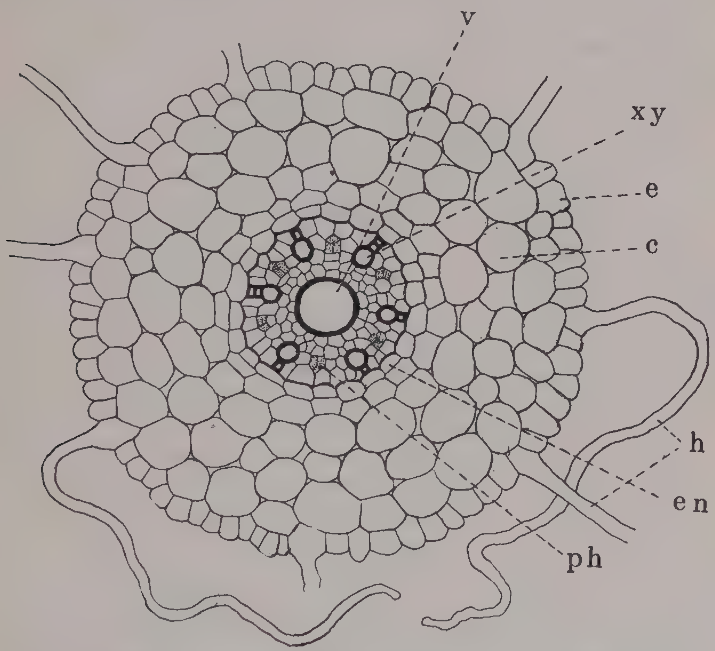

FIG. 46.—Cross section of a small root of a monocotyledonous plant; *e*, epidermis; *h*, root hairs; *c*, cortex; *en*, endodermis; *ph*, phloem; *xy*, xylem; *v*, large vessel.

Structure in Cross Section.—In a cross section through the mature root, the three parts are readily recognized; the *epidermis*, the *cortex* and the *vascular cylinder* (Fig. 46). The central cylinder of the root of an onion, for example, (Fig. 47) is surrounded by the endodermis, whose radial walls are thickened (Casparian thickening). Beneath the endodermis is the pericycle (*p*). Secondary roots arise in the pericycle. The vascular tissue consists of a circle of six masses of phloem (*ph*) alternating with six masses of xylem. In passing from stem to root the strands of phloem and xylem shift so that they lie tangentially side by side. This arrangement of phloem and xylem in the vascular region is known as the radial type of bundle.

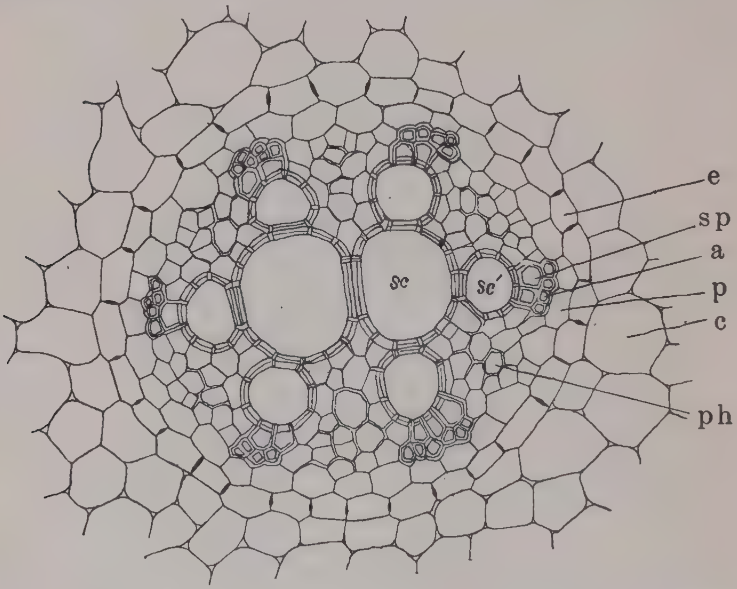

Fig. 47.—Cross section of the central cylinder of the onion root (*Allium cepa*) with cells of the cortex. *e*, endodermis; *p*, pericycle; *ph*, phloem; *a*, annular vessels; *sp*, spiral vessels; *sc*, and *sc′*, scalariform vessels.

In roots of certain plants there is a central pith.

The protoxylem (*sp*) is next to the pericycle. Proceeding toward the center from each mass of protoxylem we find a scalariform vessel (*sc′*) six in all.

In the center are two large scalariform vessels (*sc*).

In Fig. 48 is shown the mode of origin of secondary roots, or root branches.

Secondary Thickening of Roots.—Roots of most dicotyledonous plants thicken by means of secondary growth as do the stems. A cambium arises between phloem and xylem. At first it follows a very undulating course around in the vascular cylinder. It passes, for example, along the inside of a mass of phloem, then radially outwards between phloem and xylem, thence with a short curve in a tangential direction along the outer edge of the protoxylem, continuing with another sharp curve radially inwards between the next two masses of phloem and xylem, and so on until the circle is complete. The cambium ring being complete, new phloem is added on the side of the phloem and new xylem next to the xylem. Rays are also developed in the secondary layers.

As certain roots grow old and the secondary thickening just mentioned is well under way, a *cork cambium* is established in the pericycle, which produces cork on the outside and adds to the secondary cortex on the inside. After the production of the layer of cork, the primary cortex dies and eventually disappears.

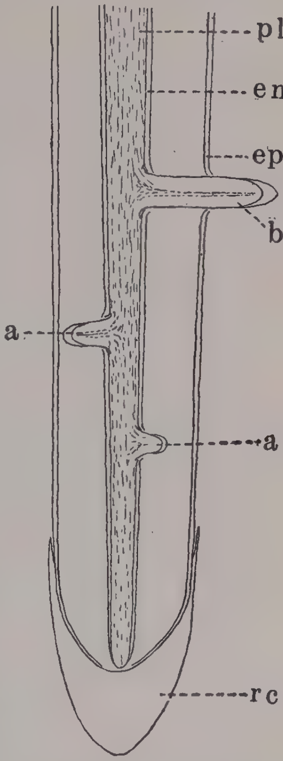

Fig. 48.—Diagram of a longitudinal section of the end of a root, showing the origin of secondary roots from the central cylinder; *rc*, root cap; *a*, *a*, young roots which have not broken through the cortex; *b*, older root; *en*, endodermis; *pl*, central cylinder; *ep*, epidermis.

Anomalous Thickening of Roots.—In such roots as the beet, several cambium rings arise in succession outside the original cambium. Each of these cambiums functions for a time, producing phloem and xylem, but the elements usually consist of thin-walled vessels and parenchyma in which food is stored.

Root of the Fern.—The root of the fern is built on the same structural plan as those of other plants with this notable exception, that the primordial meristem consists of a single apical cell in the form of a tetrahedron or

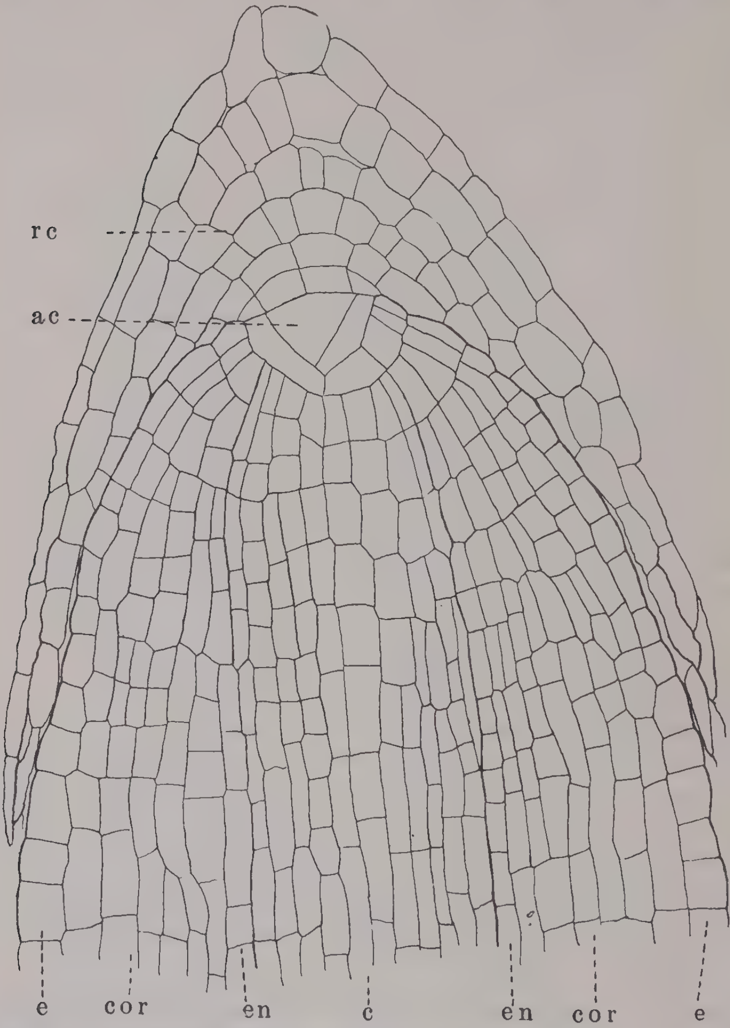

Fig. 49.—Longitudinal section through the root tip of Adiantum. *rc*, root cap; *ac*, apical cell; *e*, epidermis; *cor*, cortex; *en*, endodermis; *c*, plerome.

triangular pyramid, whose base faces the root cap (Fig. 49, *ac*). By successive divisions this apical cell cuts off segments, new cells, from all four faces. The cells cut off from the base produce the root cap, those from the three lateral faces, all the rest of the root. From each lateral cell will be formed inner and outer cells. The outer cells give rise to the protoderm and cortex which may include the endodermis. The inner cells produce the procambial cylinder. The cell divisions follow in regular sequence, the apical cell enlarging a little after each division. The cell divisions in the fern root tip are so regular that the origin of epidermis, cortex, endodermis and central cylinder may be traced with accuracy from the apical cell.

The Stele and the Vascular Bundle.—The vascular cylinder in a root or a stem is referred to as the *stele*. A stele, which may consist of one or more vascular bundles, represents all the vascular tissue developed from a procambial strand. In the growing end of the root, for example, the narrow elongating cells of the central cylinder constitute the procambial strand of the root, and the vascular tissue derived therefrom is the stele. In the ferns, for example, there are three principal types of stele: (1) the *protostele*, (2) the *siphonostele*, and (3) the *polystele*, or the dissected siphonostele, the *dictyostele*. The protostele consists of a single solid cylinder of xylem surrounded by phloem, as in the root. The protostele is regarded as the most primitive development of vascular cylinder. The siphonostele is in the form of a cylinder enclosing a central pith. In Adiantum, for example, the phloem occurs on both sides of the xylem in the pith-containing cylinder, and this stele is known as an *amphiphloic* siphonostele, as distinguished from the *ectophloic* siphonostele, in which the phloem occurs on the outside only of the pith-containing cylinder, as in the fern Osmunda. This stele, which is composed of collateral bundles, is regarded as the most advanced type, since it is characteristic of the great majority of seed plants. In the dictyostele the vascular bundles arise in separate procambial strands, without organizing into a definite cylinder. The dictyostele occurs, for example, in the stem of Pteris and in certain monocotyledonous plants (Fig. 41).

Kinds of Roots.—Based upon the manner of their origin roots are spoken of as *primary*, *secondary*, and *adventitious*. The primary root is the first root originating in the embryo; secondary roots are those which spring from the primary root. Secondary roots may branch and re-branch producing other secondary roots of higher orders, of the same system. Adventitious roots arise from other parts of the plant, as stem and leaves. Adventitious roots are common in the cereals. The numerous fine thread-like roots of plants like the grasses are called fibrous roots. Fibrous roots are usually adventitious in origin. The primary roots of corn and the cereals do not become permanent but belong to those referred to as temporary roots.

Modified Roots.—The roots referred to in the preceding paragraphs are characteristic of those organs in general. In addition to these there are many departures from the usual form, structure and function. Those that take on special structures and functions are the *modified roots*. The special structures and functions represent adjustments to some feature of the environment or to a special method of propagation. Some of the commoner modified roots may be listed as follows:

A *tap root* is a primary root which persists throughout the life of the plant and grows straight downwards. Many examples are found in Gymnosperms and dicotyledonous plants.

A *crown root* is a tap root combined with a stem of very short internodes. The internodes are so short that the leaves all seem to spring from the root, as in the dandelion, carrot, etc. Crown roots are food storage organs.

Tuberous roots are thick fleshy food storage organs, such as the dahlia and sweet potato.

Prop or *buttress roots* are developed to give stability to the stem. Examples are found in Indian corn, forest trees, etc.

Clasping or *Clinging* roots, such as possessed by the old stems of Virginia creepers, the English Ivy (*Hedera helix*) and the poison ivy (*Rhus toxicodendron*) enable the older parts of the stem to cling to flat surfaces.

Respiratory roots (pneumatophores) are those in which the extremities or knee-like bends extend above the water and convey air to parts below through lenticels or other openings. They occur in the Bald Cypress (*Taxodium distichum*), in certain palms and in some plants in mangrove swamps.

Roots of parasitic plants, as in the dodder (Cuscuta) and in the mistletoe (Phoradendron) penetrate the tissues of their hosts, the phloem and xylem of the parasite uniting histologically with the phloem and xylem respectively of the host.

CHAPTER V

ENTRANCE OF WATER AND SOLUTES INTO PLANT CELLS

Diffusion and Osmosis.—Water, mineral salts, and other compounds from which food is made, and which are necessary for all living cells, are obtained by the plant from its surroundings. In order that these materials may be utilized by the plant, they must be taken into the cells, and, furthermore, they must pass into the cells in solution, since plants do not as a rule ingest solid bodies. We may now consider some of the physical processes by which substances in solution gain entrance to the cells.

Diffusion.—If a lump of sugar be dropped into a tall, narrow cylinder of water, in a short time the lump will gradually become smaller and smaller until it finally disappears from view. We say the sugar has *dissolved* in the water. By that we mean that the particles of sugar in the solid lump moved apart and became scattered in the water. The dispersal continues, the particles becoming smaller, until they have been reduced to the size of the molecule. The molecules of sugar, therefore, are dispersed among the molecules of water.

If we should now carefully remove a little of the water from the surface in the cylinder, we should find that the water would not have a sweet taste, whereas a similar sample taken carefully, with a capillary tube, from near the bottom of the cylinder, would have a decidedly sweet taste. The cylinder is now allowed to stand undisturbed in the room for a longer time. An examination of the water after some days will show that it is more equally sweet in all parts. The particles of sugar have become evenly distributed in the water.

The lump of sugar fell to the bottom of the cylinder because of the pull of gravity, and because the lump was heavier than the volume of water displaced. The particles of sugar dispersed in all directions, up and down, and horizontally. In passing upward through the water, the force of gravity had to be overcome,—work had to be done,—and energy was, therefore, required. The energy was derived from what is called *attraction* between the sugar and the water. This attraction may be chemical in its nature; and, if so, diffusion may be a chemical, as well as a physical, phenomenon.

To sum up, therefore, let us say that by diffusion is meant the dispersal of the particles of one substance among the particles of another substance without the application of energy from the outside. The application of external energy will, of course, hasten diffusion.

If kerosene were used in our demonstration, instead of water, the sugar would not have dissolved. The attraction between the sugar and the kerosene is not of a nature to enable the particles of sugar to separate and disperse in the kerosene. The kerosene did not *wet* the sugar as water wets sugar.

Now, the particles of a gas will also disperse among the particles of other bodies. Carbon dioxide will diffuse among the molecules of other gases in the air. It will likewise diffuse among the molecules of water.

The taking in of water by a piece of dry wood, by gelatin, starch, glue, or dried apple, is a kind of diffusion termed *imbibition.*

Osmosis.—In order that substances may gain entrance to the cell it is necessary that they pass through the cell wall and into or through the plasma membrane. The passage of substances through a membrane may be demonstrated by a simple experiment. A diffusion shell is filled with sorghum molasses and closed by a perforated rubber stopper into which a glass tube is thrust. The shell is now immersed in a vessel of water (Fig. 50). In about fifteen minutes the sorghum, or a mixture of sorghum and water, will begin to rise in the glass tube and continue to do so for some hours. Water passes through the shell into the sorghum.

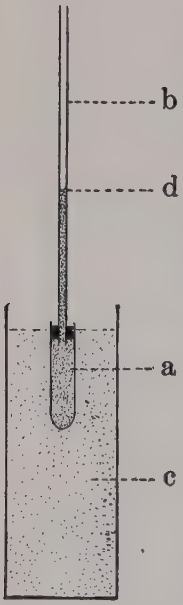

FIG. 50.—Apparatus demonstrating osmosis. *a*, diffusion shell filled with sorghum molasses, and closed with a perforated stopper. The shell is firmly tied to the stopper by means of a waxed string; *b*, glass tube thrust into stopper; *c*, jar containing water; *d*, height of liquid in the tube.

The diffusion through the membrane is known as *osmosis*. The fluid rises in the tube because the attraction of the sugar for water generates a pressure which is termed *osmotic pressure*. The osmotic pressure produced by the accumulation of water in the shell is called *turgor*, and the distended shell is said to be *turgid*, or to manifest *turgescence*.

If the apparatus be observed after several hours, the water in the jar will be slightly colored, because some of the sorghum has diffused out through the shell into the water. Diffusion into the shell is designated *endosmosis*, while that from the shell into the water is called *exosmosis*. *Diosmosis* is a term used to signify both exosmosis and endosmosis.

The shell does not permit the sugar of the sorghum to pass through it as readily as the water, and for this reason the shell is said to manifest a tendency to be semipermeable. A permeable membrane is one that will permit all substances to pass through it readily. If the sorghum should pass out as readily as the water passed into the shell, the shell would be a permeable membrane. If, on the other hand, no sorghum passed out of the shell, the shell would then be a semi-permeable membrane. Membranes which are semi-permeable are rarely encountered, but those that tend to be semi-permeable are common.

In the case of the typical plant cell, the cell wall and the plasma membrane correspond to the diffusion shell of the experiment, and the cell contents are comparable to the sorghum.

In the cell we have to deal not only with a dead membrane, the cell wall, but with a living membrane as well, the plasma membrane. There is, consequently, a profound difference between a plasma membrane and the cell wall, or the substance of the diffusion shell. A difference between a living and a dead membrane, as regards osmosis, may be demonstrated by a simple experiment. A few slices of a fresh red beet are washed in water several minutes to remove the color that escapes from the injured cells. The slices are now permitted to remain in clear water; they will retain their color, and the water will remain clear. If the water containing the slices be now heated to boiling, it will become red almost immediately owing to the fact that the red pigment, which was dissolved in the cell sap of the beet, diffused readily through both the cell wall and the plasma membrane which was killed by the heat. The living plasma membrane did not permit the color to diffuse from the cell; it tended to regulate osmosis. This fact indicates that the plasma membrane *tends to be semi-permeable.* The plasma membrane is not, therefore, like the cell wall, which is almost equally permeable to all substances in solution; but it can completely exclude certain substances while permitting others to pass through more or less readily. The plasma membrane has the power to change its permeability as the circumstances may demand. This selective power of the living membrane is manifested by the fact that different cells, or the roots of different plants, take up from the same soil entirely different compounds. One may absorb lime, another common salt, etc. The selective power of the living membrane is very apparent in certain seaweeds. In a medium containing three per cent. common salt, and very little potassium salts, a much greater quantity of potassium is accumulated than sodium.

Osmosis may now be defined as the diffusion of substances through a membrane that tends to be semipermeable. Osmosis of substances will not take place in plant cells unless the liquids in which the substances are dissolved are capable of wetting the membranes. Substances must first pass into the membrane before they can pass through it.

Plasmolysis.—We may now note one of the results of osmosis in living cells under certain laboratory conditions. If cells of some suitable plant, such as Spirogyra, or the leaf of a moss, be mounted in water and observed with the microscope, the cytoplasm containing the chloroplasts is seen next to the cell wall as a thin layer, the center of the cell being occupied by a large vacuole (Fig. 51, A). A seven per cent. solution of potassium nitrate is drawn under the cover glass. In a minute or two the cytoplasm will contract away from the wall, first at the corners, and tend to round up in the center of the cell (Fig. 51, B). Since the plasma membrane is more permeable to water than to the nitrate, some of the water of the cell has passed out through the plasma membrane, and the cytoplasm has contracted away from the cell wall because of the diminished turgor. Owing to the elasticity of the cell wall, the size of the cell has also been reduced. Some of the cell sap and the potassium nitrate have accumulated in the space between the plasma membrane and the cell wall. The potassium nitrate passes more readily through the cell wall than through the living membrane. Cells in which the cytoplasm has contracted away from the cell wall even at the corners owing to the loss of water from the cell, are said to be *plasmolyzed.*

If the potassium nitrate be replaced with water, water will osmose into the cell, and the turgor will be restored, the cytoplasm moving back into the ends of the cell, provided the living substance was not killed or injured by the nitrate. In this experiment the direction of the greatest movement of fluid is towards the side of the membrane or membranes wetted by the solution of greatest concentration. It must be remembered that cells without visible vacuoles may be plasmolyzed.

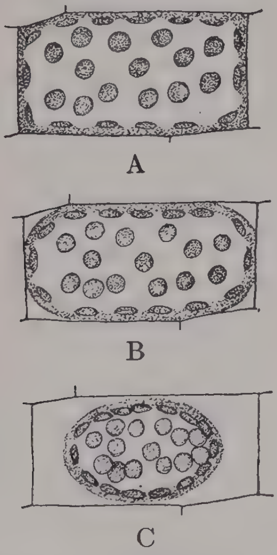

FIG. 51.—Plasmolysis of a cell. A, normal cell; B, plasmolysis has begun; C, completely plasmolyzed.

Self-plasmolysis.—Self-plasmolysis is a normal function in plant cells during certain steps in development. In the reproduction of Spirogyra, for example, the cells that unite become plasmolyzed before union (See Fig. 75, B, D). Plasmolysis cannot occur in a dead cell.

CHAPTER VI

SYNTHESIS OF FOOD—ENERGY STORAGE—ANABOLISM

Photosynthesis.—In a preceding paragraph chloroplasts were referred to as the plastids of first importance in the cell, for the reason that they, or other living portions of the cytoplasm possessing chlorophyll, are the only known parts of living cells that can make carbon compounds out of the so-called *inorganic* substances, carbon dioxide (CO_2) and water (H_2O). In short, chloroplasts may be regarded as the primary makers of organic material from these compounds. The carbon compounds made by the chloroplasts constitute the primary food materials of most plants and animals. The process by which the chloroplasts make this food is now universally termed *photosynthesis.* From the time of its discovery until more recent years (1893) the process was generally referred to as carbon assimilation.

In the process of photosynthesis certain conditions must be met. There must be present (1) the living chloroplast in cells that are under proper growing conditions, and supplied with mineral salts, such as potassium and magnesium; (2) the raw materials, water and carbon dioxide; and (3) energy in the form of normal sunlight or certain kinds of artificial light. Photosynthesis is, therefore, the process by which the living chloroplast manufactures non-nitrogenous carbon compounds out of carbon dioxide and water, in the presence of light. While the first visible product is starch, or, in some plants, oil, the first product may be a form of sugar such as glucose ($C_6H_{12}O_6$), or a very much simpler compound such as formaldehyde (CH_2O).

The manner in which this comparatively simple chemical process is accomplished is unknown at present. The reaction may be indicated as follows:

$$6CO_2 + 6H_2O = C_6H_{12}O_6 + 6O_2$$

the free oxygen being the by-product. While this simple equation indicates what may take place, it throws no light on the details of the process. Inasmuch as a molecule of glucose ($C_6H_{12}O_6$) is just six times as large as a molecule of formaldehyde, and as the aldehydes have a tendency to unite into compounds of larger molecules, it is conceivable also that formaldehyde may be condensed into glucose thus: $3CH_2O + 3CH_2O = C_6H_{12}O_6$. The supposition that two or more very simple processes are involved is strengthened by the fact that if Spirogyra, for example, is supplied with formic aldehyde in the absence of carbon dioxide, and exposed to the light, starch may be formed in the chloroplast. If a molecule of water be split off chemically from the glucose, the proportional number of the respective elements will be that in a molecule of starch, $C_6H_{10}O_5$. However starch is a very large molecule and it is written $(C_6H_{10}O_5)_n$.

Photosynthesis may be demonstrated by any one of a number of simple experiments. If from young and vigorous leaves of any suitable plant the light be excluded by an opaque paper cover for a day or longer, the iodine test will reveal no starch in the blades of the leaves. The starch in the leaves at the beginning of the experiment was removed by a process to be explained in a later paragraph. The cover is now removed, and the leaves exposed to the light. After a few hours an abundance of starch will be revealed in the leaves by the iodine test. If, instead of a large leaf, some alga, moss plant, or a shoot of Elodea, which has small, thin leaves, be used, a microscopic examination will show that the starch is located in the chloroplasts.

That oxygen is given off as a by-product in photosynthesis may be shown by suspending a shoot of Elodea, with the freshly cut end uppermost, in a glass cylinder of water, and exposing the apparatus to sunlight or good artificial light (Fig. 52, A). In a few minutes bubbles of gas will begin to escape from the cut end. The rapidity with which the bubbles are given off is a fair index of the photosynthetic activity. Or a quantity of Elodea, or some other suitable plant, may be placed in a glass vessel of water under an inverted funnel, over whose stem is suspended an inverted test tube completely filled with water. The gas given off by the plants will collect in the upper end of the tube, displacing the water (Fig. 52, B). A glowing splinter thrust into the tube will indicate the presence of oxygen, by its increased brightness. It can be shown by

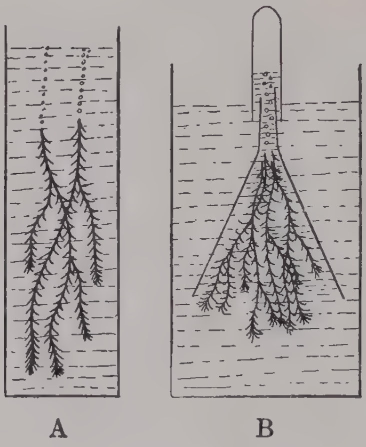

Fig. 52.—A, release of bubbles of oxygen from the cut end of the stem of Elodea in sunlight during photosynthesis. B, collection of gas, mainly oxygen from aquatic plants in sunlight during photosynthesis.

experiment that the quantity of oxygen given off is approximately equal to the carbon dioxide absorbed

$$\left(\frac{CO_2}{O_2} = 1\right).$$

Now, the synthetic process performed by the chloroplasts differs from other synthetic processes (anabolism) not only in the raw materials used, but also in the kind of energy required, which, as we have seen, is normally sunlight. Sunlight, however, is composed of different kinds of light, namely, the seven primary colors, violet, indigo, blue, green, yellow, orange, and red. When a beam of light is passed through a prism, the beam is spread out into a band colored like the rainbow. This band is called the solar *spectrum.* One end of the band shows the red colors, and the opposite end the blue or violet colors.

If an alcoholic solution of chlorophyll be examined by a spectroscope, the spectrum of chlorophyll will show two well-defined bands close together in the red end, and three broader bands, which in strong solutions obscure the violet end of the spectrum. Experiments have shown that the two bands corresponding closely to the orange bands of the spectrum of sunlight are most efficient as energy in photosynthesis. The inference is that certain rays of light, especially those of greater wave length, as the orange, or red, supply the energy necessary for the work of the chloroplasts.

Timiriazeff has constructed a curve to show graphically the relative quantities of carbon dioxide decomposed by the different parts of the spectrum. In Fig. 53 the highest point of the curve represents the most efficient rays. These have been shown to be the absorption bands in the chlorophyll spectrum which correspond to the red or orange of the solar spectrum; i.e., the bands between the Fraunhofer lines B and C. The rays of light absorbed by the chlorophyll are those that doubtless supply the energy for the work of the chloroplast.

In plants well exposed to the sun the effect of the light seems, however, to be direct, and local, diffuse light is only slightly, or not at all effective. This fact may be demonstrated by placing a heavy paper stencil over a suitable leaf, or by fastening thin pieces of cork to the leaf, and exposing it to the light. After a day or two, when the leaf is removed and decolorized, starch will be found only in those spots which have had direct access to the light (Fig. 54).

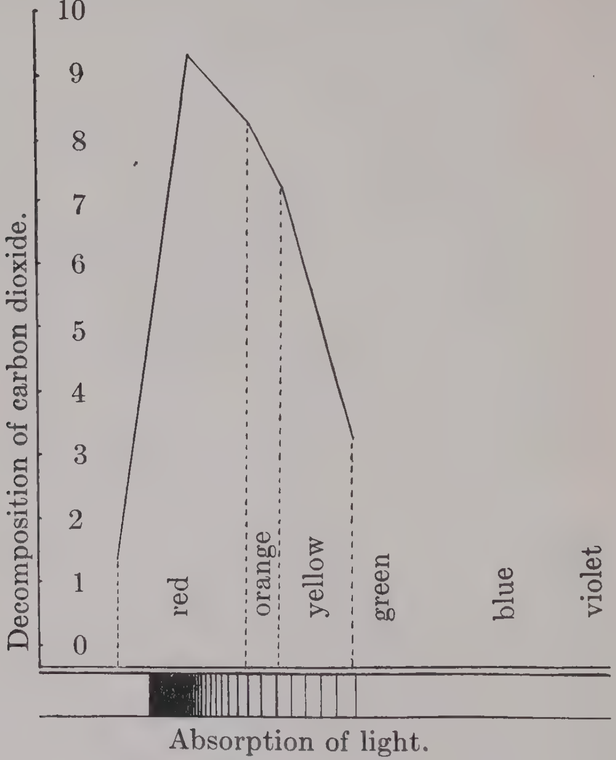

Fig. 53.—Graph illustrating the relation between the portion of the spectrum absorbed by chlorophyll and the portion most efficient in decomposing carbon dioxide. (Adapted from Timiriazev.)

Energy is just as necessary for the work of the chloroplast as it is for the operation of an engine, inasmuch as the carbon dioxide must be deoxidized, the oxygen being separated from the carbon and given off as a gas, and the carbon assembled with the hydrogen and oxygen of the water to make sugar, starch, or whatever carbon compounds that may result

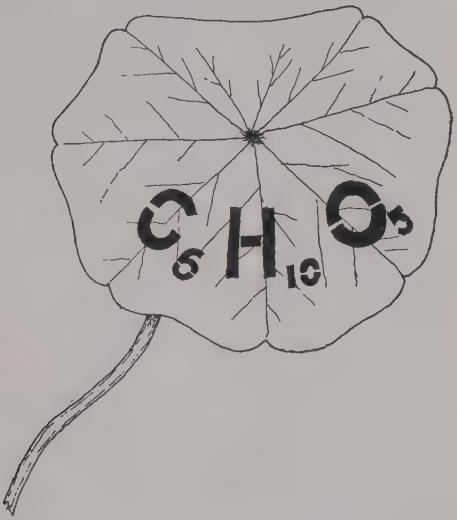

FIG. 54.—Production of starch in the illuminated parts of a foliage leaf.

In passing, it may be mentioned that whatever is necessary for the development of chlorophyll is likewise important in the process of photosynthesis. The formation of chlorophyll proceeds best with suitable light, temperature, oxygen, and the presence of iron. As magnesium is the only mineral element found in chlorophyll, it is highly probable that this element may be necessary, perhaps even more necessary, for the development of chlorophyll than the presence of iron. Chloroplasts function poorly, or not at all, in starved cells.

Photosynthesis represents, therefore, a building-up, or energy-storing process. All energy-storing processes may be included in the term *anabolism,* or *constructive metabolism.*

Other Processes of Anabolism.—We may now turn our attention to another class of synthetic activities by which complex carbon compounds are built up in cells. These differ from photosynthesis (1) in that the raw materials used are not carbon dioxide and water, and (2) in that the energy involved is not light, but it comes from within; it is endothermic. The materials, however, are primarily the carbohydrates produced by photosynthesis, while the source and nature of the energy in the cell are very imperfectly understood. These synthetic, or food-making (energy-storing) processes are collectively termed *anabolism,* or *constructive metabolism.*

Probably one of the simplest anabolic processes is the making of starch by the leucoplasts. It was pointed out in a preceding paragraph dealing with the leucoplasts (p. 17) that starch made in the leaf, of the potato for example, is changed to glucose by digestion, and transported in solution to the tuber, where the glucose is changed into starch again by the leucoplasts. The change may be expressed thus: $C_6H_{12}O_6$ + action of leucoplasts = $C_6H_{10}O_5 + H_2O$. The expression may seem to indicate that a molecule of starch is simpler than one of glucose, but the starch molecule is a very large one, as stated above, being more properly written $(C_6H_{10}O_5)_n$. This means that the carbon, hydrogen, and oxygen are combined in such a manner that for every six atoms of carbon in the molecule there are ten atoms of hydrogen and five of oxygen. In building starch from glucose the elements of the glucose are separated and recombined. As starch contains less water than glucose, a given weight of starch represents more stored energy than the same weight of glucose, just as anthracite coal represents more energy than the same weight of bituminous coal.

In a similar manner more complex carbon compounds are built up in cells out of the carbohydrates of photosynthesis. Among these may be mentioned oils and fats, such as linseed oil ($C_{57}H_{98}O_6$), castor oil ($C_{57}H_{104}O_9$), olive oil ($C_{57}H_{104}O_6$), and peanut oil ($C_{63}H_{122}O_6$), etc.*

From the foregoing it is seen that oils and fats are complex substances composed of carbon, oxygen, and hydrogen synthesized by the cell from the products of photosynthesis, and that they represent stored food, or stored energy.

Another class of synthesized products exists in what are known as amino-compounds, into whose make-up nitrogen enters, in addition to carbon, oxygen, and hydrogen. As an illustration, amino acetic acid, $CH_2NH_2.COOH$, may be mentioned. Amino acetic acid is derived from acetic acid (CH_3COOH), with one hydrogen atom replaced by the amino radicle, —NH_2.

The nitrogen is not obtained from the photosynthetic product. It is one of seven elements from which, together with carbohydrates, food, tissue-building elements, and protoplasm itself are synthesized by the cells of the plant. These seven elements, nitrogen, potassium, phosphorus, sulphur, calcium, magnesium, and iron, are obtained from the water in which the plant

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* These oils are built up by the combination of their fatty acids with glycerine, thus:

$$\begin{array}{ccccc} 3C_{18}H_{32}O & + & C_3H_8O_3 & = & C_{57}H_{98}O_6 + 3H_2O \\ \text{lineolic acid} & + & \text{glycerine} & = & \text{linseed oil} + \text{water} \\ 3C_{18}H_{34}O_3 & + & C_3H_8O_3 & = & C_{57}H_{104}O_9 + 3H_2O \\ \text{ricineolic acid} & + & \text{glycerine} & = & \text{castor oil} + \text{water} \\ 3C_{20}H_{40}O_2 & + & C_3H_8O_3 & = & C_{63}H_{122}O_6 + 3H_2O \\ \text{arachidic acid} & + & \text{glycerine} & = & \text{peanut oil} + \text{water} \\ 3C_{18}H_{34}O_2 & + & C_3H_8O_3 & = & C_{57}H_{104}O_6 + 3H_2O \\ \text{oleic acid} & + & \text{glycerine} & = & \text{olive oil} + \text{water} \end{array}$$

The molecular formulas of the above oils represent theoretically chemically pure oil. These oils as found in the plant are impure, containing other bodies in connection with the chemically pure oils.

lives, or from the water in the soil upon which the plant grows. (Plants devoid of chloroplasts are not included here.) All of these except nitrogen are frequently referred to as the mineral, or ash, constituents of plants, because they are left in the ash when the plant is burned. The nitrogen is derived from the decomposition of organic matter in the soil; or it is fixed from the air by certain bacteria that form tubercles on the roots of plants of the bean family, and by other soil bacteria.

The mineral elements enumerated above are not accessible to the plant in the free state. With the exception of the bacteria just mentioned, plants cannot utilize the free nitrogen of the air or the free mineral elements in the soil.* All of these elements must be combined with other elements in the form of soluble salts. For example, nitrogen may be accessible when combined with potassium, in the form of potassium nitrate (KNO_3); sulphur and magnesium as magnesium sulphate ($MgSO_4$); iron as iron sulphate ($FeSO_4$), etc.

The mineral salts in themselves do not constitute plant food, as the plant does not secure energy from them as such; but they play an important role in the utilization of food by the plant, and in the building of protoplasm. The several mineral elements probably play different roles in different classes of plants, or in different plants of the same class. Iron is necessary to the formation of chlorophyll in the chloroplast, but this metal is not a constituent of the chlorophyll molecule.

Among other mineral elements found in plants are sodium, chlorine, and silicon. These, while often present, do not seem to be essential. Sodium may aid in the absence of sufficient potassium. Chlorine is beneficial to such plants as asparagus. Silicon, though present in large quantities in tissues of corn, other cereals, and scouring rushes, is not known to be of much use to those plants as food.

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* It has been claimed that certain green plants are capable of utilizing the free nitrogen of the air to a very limited extent.

In addition to oils and fats and the amino compounds mentioned above, numerous and much more complex organic substances are synthesized. The nearest to protoplasm, which is in a large measure protein in character, are the protein compounds. The chemical formula for one of the proteins, *zein*, from Indian corn, has been calculated as $C_{736}H_{1161}N_{184}O_{208}S_3$. This and like expressions have very little meaning to anyone but an organic chemist. What the composition of a molecule of protoplasm is no one knows. It is highly probable that the protoplasmic molecule is more complex than that of any protein, and in active living cells it is undoubtedly a very unstable molecule.

FOOD STORAGE

Most plants manufacture, or absorb from external sources, more food than is required for immediate needs. The surplus is usually stored in the form of carbohydrates, oils, fats, amino-compounds, and proteins, such as have been mentioned in the paragraphs dealing with food synthesis. The larger quantities are found stored in those parts that are dormant or capable of becoming dormant.

In the simpler algae and fungi the zygote generally contains stored food. Materials of nutrition are often found in spores, or in parts containing the spores. Among higher plants certain parts of root, stem, or leaf are especially developed as food reservoirs. In tubers, such as the common white potato, we have stems modified into special organs of storage. In the bulb of the onion, tulip, or hyacinth, the leaf bases, which appear as thick, fleshy scales, are converted into food reservoir. In Dahlia, sweet potato, and various plants with tuberous roots, the root becomes the storehouse. In many plants reserve food may be found in parts that are not modified in any special or striking way, such as the bark and wood of trees. Seeds are among the most familiar and universal storehouses, for reserve nutritive materials in great variety are found either in the embryo or in parts surrounding the embryo.

CHAPTER VII

UTILIZATION OF FOOD—ENERGY RELEASE

In the preceding chapter we dealt with the processes that have to do with the building up of food, or the storing of energy,—constructive metabolism,—and we may now consider some of those activities concerned in the utilization of food, or the liberation of energy, namely, destructive metabolism.

Work of Enzymes.—If some barley malt be ground to a fine powder, the cell organization will be completely destroyed. The protoplasm is dead but from the dead protoplasm there may be separated by a chemical process an invisible substance which enables the plant to do a kind of work that cannot be done otherwise under conditions in which cells remain alive. The substance in question, which was separated from the malt, is known as *diastase*. Diastase is capable of doing the same kind of work when separated from the protoplasm as in the living cell. If a small bit of malt diastase be added to some very dilute starch paste in a test tube and kept in a warm place, after some hours no starch will be found in the tube. Another tube of dilute starch paste is kept under the same external conditions, but without the addition of malt diastase. In this tube, at the end of the same time, as much starch will be present as at the beginning of the experiment, as shown by the iodine test. The contents of the tube to which the diastase was added is now boiled, after the addition of some Fehling's solution. The result indicates the presence of sugar. Since no sugar was introduced with the diastase, it is clear that the starch was changed to sugar; in other words, the starch was digested. The change of starch to sugar may be expressed chemically by the equation: $C_6H_{10}O_5 + H_2O +$ energy of diastase $= C_6H_{12}O_6$. This means that a molecule of starch combined chemically with a molecule of water to make a molecule of sugar, and that the diastase helped to bring about the chemical change.

The killing of the barley plant to make malt, and the processes necessary to separate the diastase from the dead cells did not destroy the activity of the diastase. If, however, the diastase be treated with a strong acid or alkalai, or heated to the boiling point, it would have no effect in assisting the change of starch to sugar. Its action would have been completely destroyed.

Malt diastase is one of the many substances produced in living plant cells which assist in bringing about chemical changes. These substances are known as *enzymes*, and their names end in *-ase*. Each enzyme is able to do some specific thing. For example, *invertase* helps to change cane sugar to glucose and levulose; *zymase*, of the common yeast, brings about the conversion of glucose into alcohol and carbon dioxide; *lipases* act on oils and fats; *oxidases* facilitate oxidation; *protease* acts upon protein substances, etc.

A few additional examples will serve to illustrate further the character of an enzymatic action. When cultivated yeast (*Saccharomyces cerevisieae*) is permitted to grow in the presence of sugar the process of alcoholic fermentation will take place. The yeast, while feeding on the sugar, secretes an enzyme, *zymase*, which assists in a chemical change resulting in the production of two by-products, *alcohol* and *carbon dioxide*, the latter being given off as a gas. During the process heat is also evolved. Some of the energy liberated here results in the production of heat. The following equation will indicate what takes place chemically: $C_6H_{12}O_6$ by action of zymase = $2C_2H_5OH + CO_2$. If, however, the yeast be supplied with cane sugar instead of glucose, the cane sugar is first changed into more simple sugars. The yeast produces *invertase*, which assists in the chemical change expressed thus:*

$$\underset{\text{cane sugar}}{C_{12}H_{22}O_{11}} + H_2O \text{ by action of invertase } = \underset{\text{glucose}}{C_6H_{12}O_6} + \underset{\text{fructose}}{C_6H_{12}O_6}.$$

Another kind of fermentation takes place in addition to alcoholic fermentation in the complete process of making vinegar from apple cider. Through the growth of yeast the sugar in the cider is changed to alcohol. With the accumulation of alcohol and the lack of sugar, the yeast cells become inactive. Upon this alcohol some acetic acid bacterium, such as *Bacterium aceti*, feeds, and one of the results is the production of acetic acid from alcohol, as expressed in the equation: $\underset{\text{alcohol}}{C_2H_6O} + O_2$, by the activity of *Bacterium aceti* = $\underset{\text{acetic acid}}{C_2H_4O_2} + H_2O$. This process is known as acetic acid fermentation. It will be seen that acetic fermentation is an oxidizing process, inasmuch as oxygen is utilized, the molecule of alcohol being oxidized to a molecule of acetic acid. The enzyme formed by the bacterium is an *oxidase*.

Among the many processes of every day life brought about in part by the action of enzymes are the souring of milk, the conversion of cabbage into kraut, the conversion of the green fodder in the silo to ensilage, etc.

The conversion of starch into sugar, the various fermentation processes here referred to, and others too numerous to mention, represent chemical changes that are in a large measure the result of enzymatic action. The question now arises: What are enzymes?

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* Glucose and fructose differ in that the former rotates polarized light to the right, right-handed sugar, and the latter rotates polarized light to the left, left-handed sugar.

Generally speaking, let us say that enzymes are organic bodies produced in the cell, which assist in bringing about chemical changes without entering into the make-up of the compounds formed. Enzymes cannot be observed with the microscope. They are organic bodies, mostly colloidal in character, which can be precipitated by alcohol, preserved dry, or in a moist condition by the use of dilute chloroform or other chemicals preventing bacterial or fungal growth without injury to the enzymes. The action of enzymes is specific; that is, any given enzyme is capable of only one kind of activity. Enzymes are frequently referred to by group names which signify the general result, such as hydrolizing enzymes, which bring substances into solution, as the digestion of starch, and the liquefying of cell walls. Those producing oxidation are oxidizing enzymes, etc.

The activity of many enzymes, such as those producing fermentation, changes complex bodies into simpler ones, and this usually results in the liberation of energy. The energy liberated is manifested in the form of heat, in work done by the plant, and in many other ways that cannot always be readily observed or accurately measured. Enzymes that convert complex compounds into simpler ones are probably best understood. But processes that build up complex compounds, by which energy is stored, go on side by side in the cell with those that liberate energy. The glycerine used in the synthesis of oils and fats mentioned in a preceding paragraph (p. 101) was produced by the breaking up of more complex bodies. Inasmuch as there are enzymes of analysis, there are probably enzymes of synthesis also.

Up to the present time no enzyme is known to operate in photosynthesis, the source of energy here being light. In other synthetic processes, however, the energy required may be supplied in part by enzymes. In all cases of enzymatic action, it is not known whether the enzyme is the *source* of the energy or merely the *vehicle* of the energy.

Of the very many enzymes known to science, a number like diastase can be isolated and made available in commercial form.

Metabolism, Anabolism, Katabolism.—There are two great general classes of chemical changes taking place in all living organisms, which bring about opposite results. The one set of changes has to do with building up complex compounds out of simple ones. The result is that food is made and energy stored. To this class the term *anabolism* has been applied. The other class of chemical changes consists in breaking down the complex synthetic compounds into bodies of simpler composition. The result is the liberation of energy. All such chemical changes are known as *katabolism*. Anabolism, on the one hand, is food building, and energy storing; while katabolism, on the other hand, is food using, or energy liberating; and both categories taken together constitute *metabolism*. Anabolic processes are recognized by means of the visible products that can be seen, or whose presence can be demonstrated. Katabolic processes are known by their active manifestations. In the burning of a piece of wood, the organic material is oxidized, oxygen uniting with the carbon, and energy in the form of heat and light is set free, with carbon dioxide given off as a gas.

In living organisms the katabolic processes that liberate energy are included in the terms *digestion* and *respiration*. Most organisms require the oxygen of the air in respiration. Oxygen is, therefore, taken in and carbon dioxide given off. This gaseous exchange, contrary to common belief, does not constitute respiration, but it indicates, barring exceptions, that respiration, or energy release is going on.

Breathing, such as occurs in higher animals is a process of gaseous exchange. It should not be confused with respiration. It is a mechanical process like ventilation, such as the taking in of air rich in oxygen and the expulsion of air poorer in oxygen and richer in carbon dioxide.

It should be borne in mind also that respiration may be carried on in certain organisms, such as yeast, some bacteria, etc., without the presence of molecular oxygen. In such cases, however, the result of respiration is the same as in other plants.

The prevailing view seems to be that respiration implies oxidation, and that the most efficient energy release is indicated by the amount of heat produced. It is well known that energy may be liberated by the decomposition of organic substances with the liberation of heat, in other ways, as well as by processes of oxidation. Berthelot found that, with the aid of platinum black, formic acid, for example, may be decomposed with the liberation of heat, as expressed in the following equation:

$$\overset{\text{formic acid}}{HCOOH} = \overset{\text{carbon dioxide}}{CO_2} + \overset{\text{hydrogen}}{H_2}$$

The conclusion is that heat may be produced in living organisms without any connection with oxidation.

It must not be forgotten that many chemical changes can take place in plants at comparatively low temperatures, and that energy release does not necessarily imply the production of heat or oxidation. For plant life the processes included by the terms digestion, fermentation and respiration function to one end, namely, the release of energy. It is conceivable that much of the oxidation observed has to do with the *elimination of waste products*, rather than with supplying heat or the liberation of energy.

CHAPTER VIII

MOVEMENT OF WATER AND FOOD IN PLANTS

Without water life processes in plants are impossible. The amount of water in individuals manifesting life varies from that of a relatively small quantity in seeds and certain dormant vegetative tissues, to that totalling 95% to 98% by weight in certain fungi. To be sure, spores, seeds, and certain vegetative parts in the domant condition may remain alive,—they are viable; but the life processes in those structures are such that they cannot be readily demonstrated or measured by ordinary means. In the dried state those structures manifest passive life only, although all conditions necessary for the manifestations of active life are present, except a sufficient quantity of water.

In aquatic plants, in which all parts are in direct contact with water, the problem of transportation is relatively simple. The same may be said of land plants of small proportions. In regard to large plants, however, living in the air and attached to the soil, the problem is different. In the case of tall trees, water is taken in at one set of extremities, the roots, and then transported to the other set of extremities bearing the leaves, which are far removed from the source of intake. Not only must a large volume of water, with its solutes be transported to those regions in which rapid growth is taking place, and in which food is being made, but the almost unbelievable quantity lost by evaporation from the leaves and all other tender parts in contact with the air must be replaced.

Transpiration.—The evaporation of water vapor from the surface of the live parts of plants is termed *transpiration*. The fact that a large quantity of water is given off as vapor from leaves and other tender parts exposed to the air can be readily demonstrated by one of many simple experiments. For example, if a leaf of any suitable plant be supported by a piece of stiff paper, through which the petiole extends into a glass of water, and then covered by another glass, as shown in Fig. 55, the whole being placed in sunlight, in a few minutes vapor will be visible on the wall of the inverted glass. In a comparatively short time the condensed moisture will collect in drops and run down the sides of the glass.

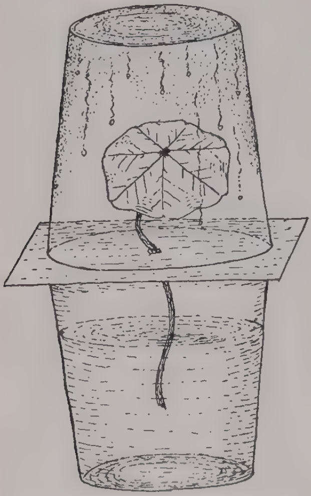

Fig. 55.—Apparatus to demonstrate the evaporation of water from a leaf.

With the proper use of suitable apparatus, the quantity of water transpired by a leaf, or by a whole plant, in a given time may be determined approximately.

The amount of water evaporated from the leaves is surprisingly large. It has been estimated that a strong sunflower plant about six feet tall will evaporate on a warm day over a liter of water. An acre of cabbage will give off two millions liters of water in four months. Calculations tend to show also that for every gram of dry, solid matter produced in some plants, 250,900 grams of water are evaporated.

In short, the process of transpiration takes place in the following manner: The epidermal cell wall exposed to the air loses some of its water by evaporation. By imbibition the wall replenishes its supply from within the cell. The epidermal cell, having lost water, will, by osmosis, replenish its supply from the cell or cells beneath, which are not transpiring, or only at a much slower rate. This process will continue into deeper lying cells until those are reached which are in contact with the xylem of the vascular bundle, from which a constant supply of water is provided.

Our study of leaf structure has shown that the leaf has also an internal surface, namely, the cell surfaces abutting upon the intercellular spaces. From this internal surface evaporation will take place under certain conditions. In the epidermis of the under side of our typical leaf are the many minute pores, the stomata. The number of stomata is surprisingly large. A medium-sized cabbage leaf is provided with about seven million, and a sunflower leaf with approximately thirteen million. When the pores are open, the moisture in the intercellular spaces escapes, as may be demonstrated by placing bits of cobalt paper, an indicator for moisture, against the lower surface of the leaf. (Cobalt paper, which is blue when dry, becomes rose-colored when moist.) If the pores are closed, very little or no moisture will be given off, the cobalt paper remaining blue. The guard cells are able to open and close the pores under certain conditions. When the stomata are open, transpiration is at its maximum; when they are closed, transpiration sinks to near its zero point. Because of this behavior of the guard cells, the leaf is able to control transpiration to a certain degree. During bright, warm, sunny weather, with a certain degree of humidity in the air, the stomata are wide open; darkness and dry air, on the contrary, tend to close the pores. The wilting frequently observed in broad-leaved plants during the warmer hours of bright, sunny days is due to excessive transpiration. While the water evaporated from the surface of epidermal cells is considerable, the quantity lost by the leaf through stomatal transpiration is very much greater.

Not only does the leaf tend to regulate stomatal transpiration in the manner just mentioned, but surface evaporation in general is diminished by the presence of cutin and wax in the outer epidermal walls. The cuticular layers may be so thick that evaporation is scarcely observable. Corky walls act in a manner similar to cuticularized walls. Various fruits, such as apples, pumpkins, melons, and vegetative parts, such as potatoes, etc., remain fresh though severed from the plant, because of the water-proofing of the corky or cuticularized layers. The evaporation of water from the surface of the plant is a physical process that takes place in some degree at all times. While the plant may tend to regulate transpiration, it cannot stop it altogether.

In some cases, as when the relative humidity of the air is low, when the soil is dry, or when the roots of the plant have been disturbed, transpiration may reduce the water content of the plant to a point where serious injury, or even death, may occur. In fact, the relation between the rate of transpiration and the water supply is the limiting factor of agriculture in many regions otherwise favorable. It is hardly conceivable that a process involving the movement of such quantities of water, and so intimately connected with the welfare of the plant, should be without meaning. What, then, is the significance of transpiration?

One of the earliest theories propounded in answer to this question was to the effect that transpiration is instrumental in keeping the plant cool. This was based on the analogy between transpiration in plants and perspiration in animals. Tests that have been made indicate that transpiration may keep the temperature of the leaf as much as five degrees (C.) lower than that of the surrounding air, and this difference may be of incidental significance to young, tender leaves, but it is believed that the real meaning of the process must be sought elsewhere.

Another theory assumes that the dilute mineral solutions taken in by the roots of the plant must be concentrated before they can be used in making food; and transpiration is cited as a process of concentration which makes these solutions ready for use. But most investigations on diffusion and osmosis indicate that water and dissolved substances pass from cell to cell independently of one another, and that any concentration which does occur in a cell could be effected without transpiration.

Both of these theories fall short when applied to a set of conditions widespread in nature. On any occasion when the temperature is high and the soil very wet, transpiration should for the welfare of the plant be most rapid, according to these theories, because the plant would most need its cooling effect, and the mineral solutions taken in through the roots would be most dilute. But observation readily shows that on such occasions transpiration is reduced to the minimum because the relative humidity of the air is high. And yet it is on just such occasions that plants grow most luxuriantly. The warm, humid regions of the Amazon valley, the southern slope of the Himalayas, and such tropical islands as Ceylon, Java, and Borneo are exactly adapted to a low rate of transpiration, and they have the most luxurious vegetation in the world. In our own climate plants grow best on the hot, sultry days of summer, when the air is so moist that there is little transpiration. From these evidences it would seem that transpiration is not a definite function, that is, a thing that is conducive to the well-being of the plant, but a thing to be avoided if possible.

There is such a close correlation between transpiration and the conditions favorable for ordinary evaporation as to suggest that the two processes are the same thing. Practically every case of lack of correlation between the two can be satisfactorily explained by data on the available water supply, the osmotic properties of the water supply, and the behavior of stomata or other devices modifying the rate of transpiration.

Viewed in this light it would seem that our ordinary land plants would have been more fortunately designed if their aerial parts had been covered with a layer of some kind of material impervious to water; but this would have interfered with another important function. Carbon dioxide is necessary for photosynthesis, and it is secured chiefly from the air. On final analysis carbon dioxide can be secured by the aerial part of a plant only by exposure of a moist membrane to the air. The very door that is opened to admit carbon dioxide unavoidably lets water escape; and this is transpiration.

The whole complicated process may be looked upon as a case of barter between the plant and its environment. The plant must exchange more or less water for any carbon dioxide that it gets. If the air is moist, less water is given off; carbon dioxide is secured at the cost of little water; and much food is made. If the air is dry, a much larger amount of water is given off incident to the securing of the same amount of carbon dioxide. On hot, dry days the plant may even close its stomata, or roll its leaves, until the return of better conditions. Desert plants live in a perpetual condition of insufficient moisture, and their necessary frugality results in slow growth.

A mechanical explanation is usually available for each of these activities. The air that would be most injurious to the tissues of the leaf, because of its dryness, is instrumental in closing the stomata or stimulating to action other protective devices. The moist air that will do the minimum of damage to the inside of the leaf, works in the reverse order.

Exudation of Liquid Water by Leaves.—Not only do leaves continuously throw off water in the form of vapor, but in many leaves liquid water is forced out through the water pores or water glands. This is especially noticeable in the young leaves of many plants. To demonstrate this fact all that is necessary is to enclose in a moist chamber a small potted plant of the dwarf Nasturtium or some seedlings of Indian corn. After a few hours, clear drops of water will be seen hanging from the edge of the younger leaves at the ends of the large veins, or from the tips of the young blades of corn. Or in early morning, following a still, clear night, similar drops may be observed on the leaves of plants in the open, such as tender blades of grass, young leaves of the grape vine, etc. This water is exuded by peculiar structures between the ends of the veins and the epidermis, known as the *epithema*. The epithema consists of living cells in which the tracheids terminate. In the overlying epidermis are peculiar pores called water pores, or water stomata. The water pores are much larger than ordinary stomata, and their guard cells remain permanently open. The water exuded frequently contains, among other substances, calcium carbonate, which may remain as an incrustation over the water pores.

It is possible that in submerged water plants exudation may function in the same manner as transpiration in maintaining the current from the absorbing organs.

Root Pressure; Bleeding.—Another phenomenon concerned in the movement of water in the plant is seen in what is termed *root pressure*. In many plants water is seen to be exuded when wounds are made or stems cut off. It is especially marked in the grape vine if it is pruned too late in the season. From the cut end of the vine water will drop in considerable quantities. The phenomenon is known as "bleeding." The water comes from the vessels, and it is forced out by the activity of the roots styled *root pressure.* The flow of sap when a sugar maple tree is tapped in late winter or early spring is due, in a large measure, to root pressure. The quantity of water is great in the maple, grape, birch, and palms. The out-flowing sap contains mineral salts and large quantities of organic substances. The sap of the sugar maple contains about ½% of common sugar.

Root pressure may be readily demonstrated by a simple experiment, in which a glass tube is substituted for the larger part of the stem. The stem of Dahlia, or other suitable plant, is cut off within a few centimeters of the ground, and, by means of a short piece of rubber tubing, a glass tube of small bore is attached water tight to the end of the stem connected with the roots, as shown in Fig. 56. In a few hours, water forced out through the end of the stem by the activity of the roots will rise in the glass tube and may continue to do so for a number of days.

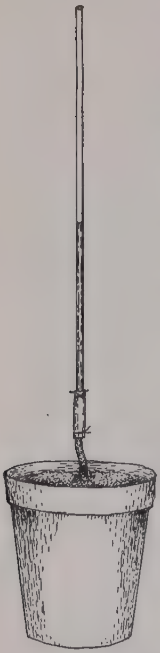

FIG. 56.—Root pressure. A glass tube has been substituted for the stem of the plant, and water has risen some distance in the tube. This demonstrates one of the causes of the ascent of sap.

The Conduction of Water.—The water given off by the plant by transpiration or by exudation was taken up by absorbing organs and then transported to the evaporating surfaces or to the organs of exudation. In the lower plants, or in those of small size and simple structure, osmosis and diffusion from cell to cell may suffice for adequate transportation. But in the higher plants other processes and a special conducting system are involved. In a foregoing chapter it was pointed out that the vascular tissue functions as the system of rapid transit for the conduction of liquids. The root hairs absorb water and mineral salts from the soil, and by diffusion and osmosis, this water is conveyed from cell to cell of the cortex of the root to the xylem of the vascular bundles, through which a continuous stream is rapidly transported to the most remote extremities of stem and leaves.

Rôle of the Xylem.—That part of the vascular bundle which transports water and dissolved substances from roots into the plant is the xylem, and this fact is easily demonstrated. We usually think of the xylem as conducting the water upward in the plant, or from base to tip, but the direction may be readily reversed. If a branch be removed from a suitable woody plant and supported with the cut-off tip end in water, it will be seen that the water now moves in the reverse direction, i.e., from tip to base. If the stem be girdled, and colored water, such as a dilute solution of eosin, be used, it will be observed that the water does not pass through the bark, which contains the phloem of the vascular bundles. The xylem transports not merely water and dissolved salts, but digested food as well. Chemical analysis has shown that the vessels of the xylem, especially in the spring, may contain sugar, protein, and amides (nitrogenous food of simpler composition than proteins). At other times of the year these compounds are present, but in smaller amounts. Notable examples are the maples and birches.

Function of the Phloem.—It is very evident that in many plants the bulk of the plastic food is made in parts of the plant that are remote from the parts in which the food is used or stored. The surplus food made in the leaves and other green parts is transported to regions of growth and storage, and stored food, in turn, must be transported from the storage organs to the growing tissues.

It can be shown that the elements of the phloem, especially the sieve tubes, contain, along with other substances, carbohydrates, proteins, and amides, in large quantities; and it is easily demonstrated that these substances are conducted upwards or downwards in the stem by the phloem. For example, a willow cutting is girdled by the removal of a ring of bark a short distance from its lower end, and supported in an upright position with its lower end in water (Fig. 57). In due time the cutting will send out roots and shoots. From the part of the stem below the girdle the development of roots especially will be much less extensive than above the girdle. Moreover, no food will be stored in the bark or cortex below the girdle.

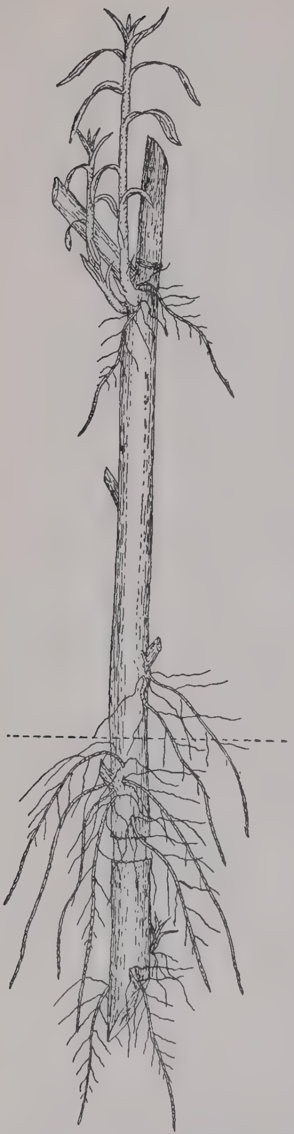

Fig. 57.—Roots and branches developed by a girdled stem of the willow. The cutting was kept in water up to the dotted line.

The sieve tubes are well adapted to the conduction of proteins and other colloids, which diffuse throughout the cell and through the cell walls with difficulty. The office of the companion cells is not so well understood. They may take over materials from the sieve tubes and pass them on to other structural elements for immediate use or storage. It is not improbable that companion cells may also act as glands to change substances in the sieve tubes, or after they are taken over to be passed on. The phloem parenchyma seems to be well fitted to conduct carbohydrates and amino compounds in a longitudinal direction and turn them over to the vascular rays for storage and for transportation in a radial direction in the stem. The phloem parenchyma, and the parts of the vascular ray most resembling phloem, are the principal places of the storage of protein during the dormant periods of winter and dry seasons.

The Ascent of Sap in Tall Plants.—Attention has been called to the necessity of the transportation of water and solutes from the absorbing ends of roots to the most remote extremities of the branches, the leaves, a distance of as much as 95 or 100 meters (311 to 328 feet) in the case of the tall Sequoia and the Eucalyptus. The question of what causes the ascent of sap in tall plants still awaits a satisfactory answer, and the best that can be done here is to point out the important processes that are known to operate in the plant.

As soon as the seedling emerges from the soil and expands its first leaves, a continuous column of water is established, and it moves upwards through the xylem of stem and branches from the absorbing ends of the roots to the leaves, where water is being given off continually by transpiration. This column of water is known as the transpiration stream. The transpiration stream is, therefore, established in the very small plant and persists until the plant dies and dries out. During the winter, when the plants are dormant, very little water is transported, as compared with the time of full foliage in spring and summer.

Attention has also been called to the large amount of water given off by the leaves in transpiration, and the fact that water is forced into the plants by the work of the roots known as root pressure. It can be shown experimentally that, during active transpiration especially, the water and bubbles of gas in the vessels of the xylem are under tension; the transporting stream is being stretched. If one cuts in two under mercury the stem or branch of a rapidly transpiring plant, it will be found that the mercury is sucked rapidly into the vessels from the cut surface. The phenomenon is referred to as *negative gas pressure,* and it is most pronounced on warm, sunny days which favor transpiration.

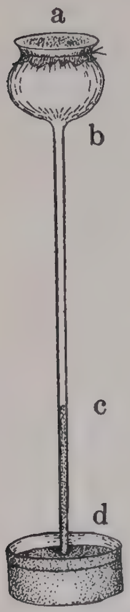

FIG. 58.—Apparatus to show suction caused by evaporation of water through a membrane. *a*, membrane; *b*, thistle tube containing water; *c*, height to which mercury has risen; *d*, dish of mercury.

That transpiration develops a suction, or lifting power, can be demonstrated by a very simple experiment. A thistle tube with the large end closed by a membrane, such as prepared bladder, is completely filled with water, and supported in a vertical position with the open end of the tube in a dish of mercury (Fig. 58). After a time the mercury will have risen in the tube. Water passes out of the tube by evaporation from the surface of the membrane, and mercury rises in the lower end to take the place of the evaporated water. The mercury is forced up into the tube by the pressure of the air. The evaporation from the surface of the membrane brings about a suction, or lifting power, in the same manner as transpiration from leaves tends to stretch the column of water in the xylem. It must be borne in mind that this simple experiment does not show, and it is not intended to show, the cohesive strength of liquid water. It shows that evaporation can produce a lifting power, or suction. Suitable experiments, however, have shown that the cohesion of liquid water is a very important factor in the movement of the transpiration stream.

By way of summary, it may be stated, therefore, that the chief underlying causes of the movement of water in the stems of plants are transpiration from the leaves, imbibition of cell walls, cohesion of liquid water, and root pressure.

In discussions of the movement of water, root pressure is doubtless underestimated, owing to the fact that it is not apparent when transpiration is active. That root pressure seems to be absent during rapid transpiration may be due to the fact that transpiration is pulling so much harder than root pressure is pushing that the latter is not observed or does not show in the experiment. An automobile with just enough gas supplied to idle the engine in going down grade will, by its momentum, push harder than the engine is pulling, but that does not prove that the engine does not pull at all.

CHAPTER IX

GROWTH AND RESPONSES TO STIMULI

The term *growth* usually carries with it the idea of increase in size, which implies also an increase in weight of dried material. An increase in size of the plant, or any part of it, may not be accompanied, however, by an increase in dried substance; on the contrary, plants may lose in the weight of dried material while increasing greatly in volume, the increase in size being due to the accumulation of water, or *growth by hydration.* Seedlings grown for some time with their roots in clean sand or in pure water, especially if they are kept in the dark, will increase greatly in volume, but lose in dry weight. The dried substances present in the seed are consumed by katabolic processes involved in the release of energy. Growth under such conditions does not lead to the continued normal development of the plants, but to its exhaustion and death.

About half a century ago the distinguished botanist, Sachs, recognized growth under three phases: (1) the embryonic phase, in which the beginnings of new parts or organs are formed; (2) the phase of elongation or enlargement of parts already formed; and (3) the phase of internal development and completion of the tissues. To use less formal statements, let us say that growth signifies the *forming*, *unfolding*, and *maturing* of the plant or its parts. These three steps occur in the development of all plants, no matter how simple or how complex in structure.

It should be understood that these phases are not sharply separated, but they merge into one another imperceptibly; for in a growing shoot in the summer, the forming of new parts, elongation, and maturing of previously elongated parts, go on simultaneously.

These three steps are well illustrated in the branch of a pine tree. During the previous season the bud at the end of the branch was formed (Fig. 59, left). At the growing point there took place in the embryonic tissue of the end of the stem the division of cells and their arrangement into the primordia of the parts present, namely, scale leaves, dwarf branches and foliage leaves (needles), frequently flowers, and new buds. When growth begins in the following spring, these parts unfold, and the new shoot appears with an apparent suddenness

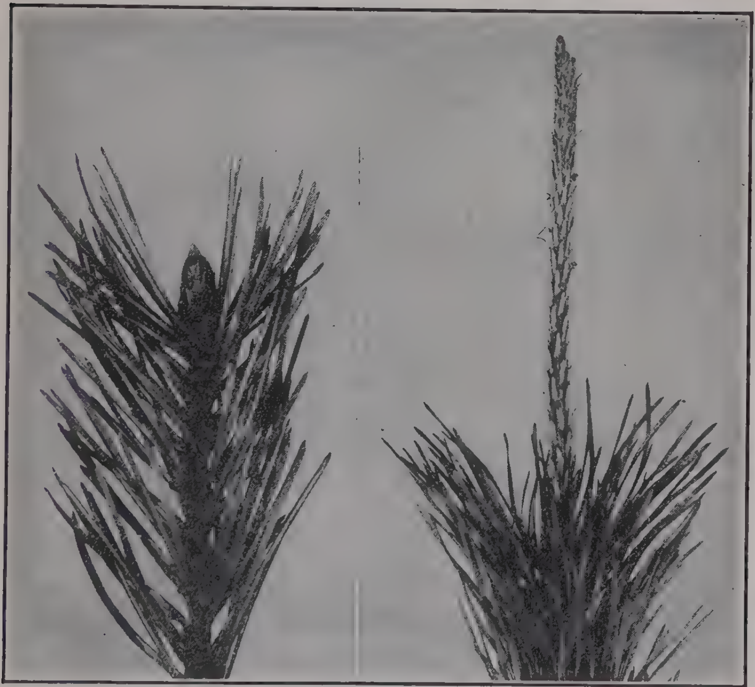

Fig. 59.—End of pine branch with winter bud at the left. At the right, the stem and leaves are rapidly elongating.

(Fig. 59, right). The unfolding is due to the increase in size of the cells, owing chiefly to the accumulation of water. This is the phase of growth that is usually measured by growth-recording apparatus. It must be remembered that growth by accretion is likewise subject to measurement.

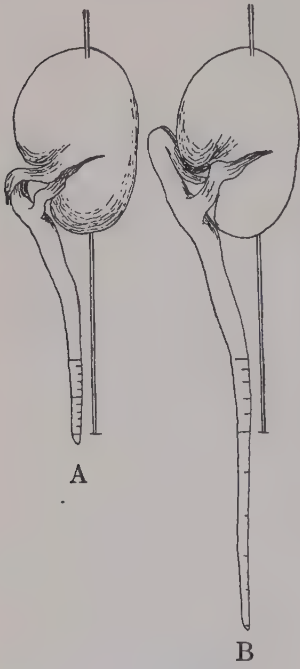

Fig. 60.—Region of elongation in growing root of seedling of the broad Windsor Bean (Vicia faba). A, the end of the root is marked with india ink at intervals of about 1 mm. B, the same root 24 hours later. The distance between the marks indicates that the region of greatest elongation lies within the first few millimeters back of the root cap. (From Strasburger.)

In many plants the total effect of growth by hydration is very striking, as when a mushroom "springs up in the night" due to the elongation of the cells of its stalk and cap, or when a bush becomes green in foliage in a day, owing to the enlargement and unfolding of the parts in the winter bud. It is said that the filaments of the stamens in the flowers of certain grasses (particularly the bamboos) elongate as rapidly as the movement of the minute hand of a watch. In the case of the bamboo, however, the growing zone is of considerable length, whereas the percentage of growth is much lower than in the case of certain fungal filaments and pollen tubes.

The part of the plant that elongates, in root or shoot, for example, may be readily located by placing on it at definite distances marks made with waterproof ink, as shown in Fig. 60, A. The root of a seedling so marked will appear after 24 hours as seen in Fig. 60, B. Where no elongation has taken place the marks remain the same distance apart as in the beginning of the experiment; but in the elongated portion distances between the marks have very noticeably increased.

Thus we see that in a root the region of elongation is confined to a portion a few millimeters in length just back of the apex covered by the root cap.

In a like manner the region of elongation in a stem is found to be confined to a distance of a few nodes and internodes back of the growing point.

Following elongation, the cells of the larger part of the branch or root mature. Their walls may be greatly thickened, and food may be accumulated in certain cells. These are processes of accretion, as distinguished from hydration. The ends of growing members, as stems and roots, are characterized by the presence of embryonic cells. In gymnosperms and in dicotyledonous angiosperms, embryonic tissue is continued back into the older parts between phloem and xylem, where we have learned to know it as cambium. Cells capable of growth and division occur also in older and adult tissues.

Root Pull.—While growth usually implies an increase in length, yet just the reverse may occur during the maturing of some roots. The tap root of the Broad Bean (*Vicia faba*), for example, shortens appreciably during the internal development of the older parts, as is evidenced by a wrinkling of the surface of the root a short distance below the cotyledons. This phenomenon is known as *root pull.* A notable example is found in the Skunk Cabbage, in which the older roots, by shortening, tend to keep the stem down in the soil. Root pull is also illustrated in the Jack-in-the-Pulpit (*Arisaema triphyllum*), in the common dandelion, and in many other plants.

Work Done in Growth.—The work done by growing organs is often very great, as measured by its cumulative effect. Roots of trees pry apart ledges of rock or split off fragments requiring an amount of energy equivalent to a lifting power of tons. By a simple experiment, the root of a bean may be shown to develop sufficient energy to split a plast cast (Fig. 61). Or the growing leaves of a fern are capable of bursting a thin crust of overlying concrete. In daily life instances of the work done by growing roots and stems are frequently encountered.

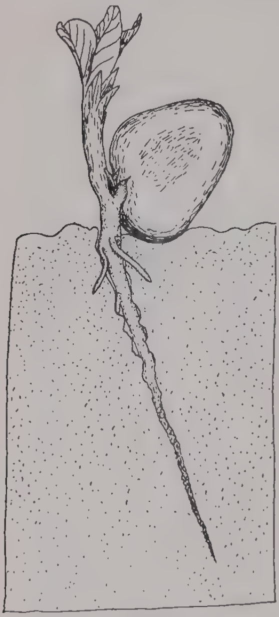

Fig. 61.—Mechanical work done by a growing plant. Root of Windsor Bean bursting a block of gypsum in which it has been embedded.

PLANT RESPONSES

One of the most marked differences between living organisms and inert objects is the fact that the former respond to stimuli in a manner very different from the reactions of non-living matter. Plants and plant parts seem to adjust themselves to one another, to their immediate neighbors, and to other forces of the environment that affect them as stimuli.

Motile plants, or motile plant cells, manifest their responses in changes in the direction of locomotion, while those that do not have the power of locomotion respond by means of growth curves. The response made to a given stimulus is usually designated by a term implying the character of the stimulus, as, for example, the response made by a plant organ to gravity is termed *geotropism;* to light, *phototropism;* to moisture, *hydrotropism,* etc. When the direction of the response is toward the source of the stimulus, it is designated as *positive.* A response in the opposite direction, or away from the source of the stimulus, is *negative.* A few plant responses will be dealt with in the following paragraphs.

Geotropism.—Plants adjust themselves with reference to the force of gravity. This response is known as *geotropism.* Roots tend to grow toward the center of the earth. They are positively geotropic. Stems, which grow in the opposite direction, are negatively geotropic. Roots or branches growing horizontally are *diageotropic.*

It is readily shown by experiment that if a root or a stem be inclined from the normal position with reference to gravity, as when placed horizontally, the root will curve downward and the stem upward. The place of curvature coincides with the region of greatest elongation; hence such curvatures are growth curves. The curving organ grows faster on the convex side than on the concave side. In fact, the concave side may sometimes be shortened.

In the case of the root, the stimulus of gravity is perceived by the growing point and the root cap, and transmitted to the region of elongation, where curvature takes place. If the tip of the horizontally placed root be cut off carefully with a sharp razor, the root will elongate, but it will not curve, until by regeneration a new growing point is established.

Phototropism.—We may see about us every day that leaves on a plant so adjust their positions with reference to one another that there is the least possible interference with their illumination. The leaves of the Virginia creeper, which spreads on the side of a building, or other support, exhibit a sort of mosaic as mentioned in Chapter II. In fact such arrangements are known as *leaf mosaics.* When a potted plant is removed from its normal position out of doors, where it is illuminated more equally on all sides, to a place near a window, in which illumination comes largely from one direction, the plant will curve toward the light, and become so placed that the upper surfaces of the eaves are exposed more nearly at right angles to the direction of the impinging light rays. Plant organs that are positively phototropic in one stage of their development, and negatively phototropic in another, are not uncommon. The flower pedicel of the Kenilworth ivy (*Linaria cymbalaria*) is positively phototropic up to the time of the opening of the flower, but as the fruit is maturing the pedicel becomes negatively phototropic and thrusts the pod into a crack or cranny of the substratum.

A combined geotropic and phototropic response may be demonstrated by placing an inverted plant near the window in a room, where the adjustment of leaves and stems involves responses to both light and gravity.

Response to Contact, Thigmotropism.—The younger branches of the Virginia creeper cling to the wall of a building by means of branched tendrils which are modified stems. The ends of the tendrils become modified into holdfasts when they come into contact with a rough surface. In response to contact with the wall, the cells of the holdfasts thus stimulated grow and become wedged or dove-tailed into the minute depressions of the surface, and the tendrils are firmly anchored to the wall. From one point of view the holdfast may be said to possess a sense of touch. It is of interest to note that from the older parts of the stem of the Virginia creeper, modified roots also become organs of attachment and respond to the stimulus of contact.

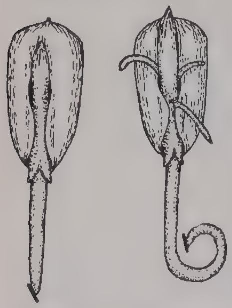

Fig. 62.—Traumatic Response. A small bit of paper fastened to one side of the tip of the root causes the root to curve in growth away from the source of irritation.

Response to Injury, Traumatropism.—The response which a plant organ makes to injury is known as *traumatropism.* If a bit of paper be glued to one side of the growing end of a root tip, or if the growing point be wounded by cutting away with a sharp razor a thin tangential section, or by searing with a hot glass rod, and the seedling with the root thus injured be supported in moist air so that growth will continue, after several hours the end of the root, in successful experiments, will have made a sharp curve away from the side injured (Fig. 62).

Hydrotropism, and Rheotropism.—Plant organs respond to moisture in the form of vapor, and to currents of water. The response to currents of water is called *rheotropism.*

Responses Due to Changes in Turgor.—These responses differ somewhat in character from those mentioned in the preceding. One of the most familiar is seen in the sudden leaf movements of the sensitive plant (*Mimosa pudica*). Stimulated either mechanically or chemically when expanded, the leaflets of this plant close up together in pairs, and the whole leaf suddenly sinks to an almost vertical position. At the base of the petiole of each leaf, and at the base of each leaflet, there is a joint known as the *pulvinus.* When the leaf is stimulated by shock or otherwise, this stimulus is transmitted to the pulvinus, and the cell sap of the cells on the lower side suddenly escapes into the intercellular spaces, and this side becomes flaccid and shortens because of decreased turgor. The cells of the upper side, which have retained their turgor, cause that side to elongate, and the whole leaf is forced into a downwardly inclined position. Movements of this character are known as *turgor movements.* They are not growth curvatures in the sense in which growth has been used in preceding paragraphs.

Chemotropism, Chemotaxis.—Responses made to stimuli resulting from chemical substances are many and varied. Certain reproductive cells of many plants are very sensitive to dilute chemical solutions. The sperm of the fern, for example, is known to respond to several chemical substances, one of which is malic acid. The sperms of an ordinary fern will flock into a capillary tube filled with a dilute solution (.1% to .01%) of malic acid with the same alacrity as when they enter the plant organ containing the egg, with which a sperm ordinarily unites.

When the response is concerned with free-swimming cells instead of stationary parts, the term *chemotaxis* is used. Chemotactic responses play a very important role in bringing reproductive cells together, and in directing the growth of plants and plant organs.

Autonomic Movements.—There is another class of movements not due to external stimuli but to internal causes. One of these is known as *nutation.* A stem or shoot, for example, does not grow upward following a straight course, but as it grows it continually curves in one direction, describing a sort of spiral. This may be recognized in a rapidly growing upright shoot in that the shoot seems to lop over as if it were wilting. Continued observation will show that the curved shoot does not always point in the same direction. A record of the movement of the end of the shoot indicates a spiral course.

Successive Opening and Closing of Flowers.—The opening of such flowers as the Crocus and Tulip during the day and closing at night, or during cool, cloudy daylight, are due to alternating growth on the upper and lower sides at the bases of the segments of the perianth.

There are many other kinds of plant responses, but those mentioned in the foregoing, which fall under common observation out of doors or in the laboratory, will serve to illustrate the manifold sensitiveness of living things.

CHAPTER X

MYXOMYCETES AND SCHIZOPHYTA
SLIME MOULDS—FISSION PLANTS

The slime moulds comprise a group of low organisms on the border line between plants and animals. In their vegetative, or assimilative phase, the *plasmodium*, they bear certain resemblances to the microscopic, one-celled animal, the amoeba; but in the reproductive, or spore-producing, phase they reveal very definite and pro-

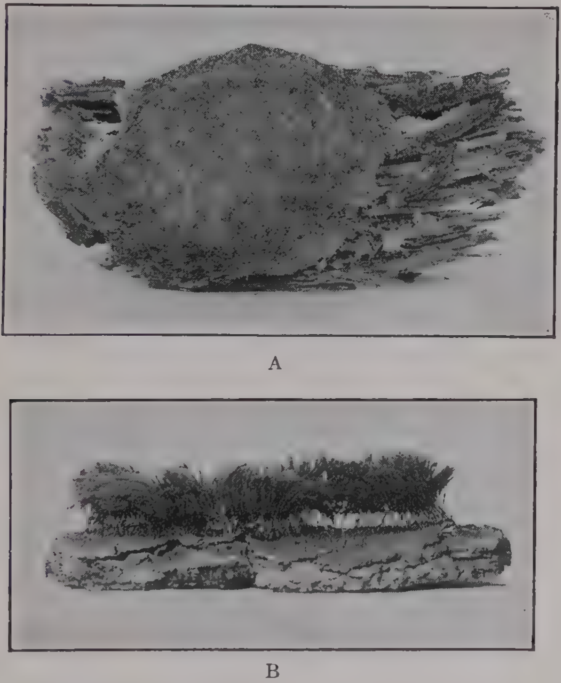

Fig. 63.—Fruiting phase, spore-bearing parts, of slime mould. A, *Fuligo ovata* (Schaeff.) Macbr.; B, *Stemonitis morgani* Peck. × 1.

nounced plant characteristics. In their reproductive phase the larger forms are commonly recognized as yellowish or light-colored, cake-like masses on such objects as decaying logs and stumps, the planks of walks, spent tanbark, decaying leaves, and apple pomace. These large spore-bearing masses may have a brittle, limy crust, as in Fuligo (Fig. 63, A), while in others the mass is provided with a firmer, skin-like cover, as in Lycogola (Fig. 64, A). In the spore-producing phase some of the large species were mistaken by the earlier botanists for puff-balls.

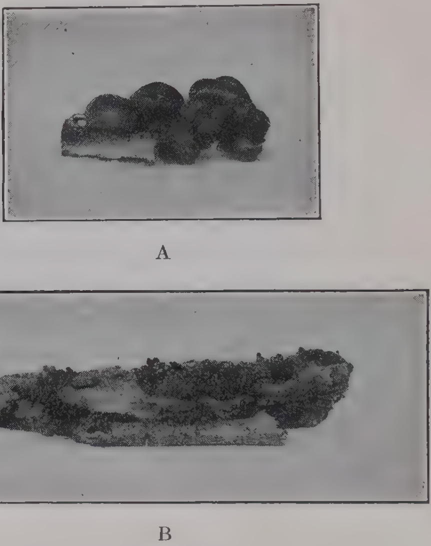

FIG. 64.—Spore-bearing part (sporangia) of slime moulds on decaying wood. A, *Lycogola epidendrum* (Buxb.) Fr.; B, *Hemitrichia clavata* (Pers.) Rost. × 1.

The vast majority of the slime moulds, however, develop small and very beautiful reproductive bodies that are recognized only by those having had some training in their observation.

The Plasmodium, or Vegetative Phase.—The plasmodium of a typical slime mould consists of a naked, multinucleated mass of protoplasm that creeps or flows through the crevices and interstices of the decaying wood, leaves, soil or other substratum on which it happens to be growing. Generally the plasmodium appears as a thick, sticky or slimy, yellowish or creamy mass within the substratum, or as it oozes out upon the surface. Though the color be prevailingly yellow, it may be brown, red, violet, or almost any tint, even greenish. In Fig. 65, there is represented a portion of a plasmodium which crept over the inner surface of the wall of a bell jar used as a cover for a piece of decaying wood on which the plant was growing. The piece of wood was placed under the bell jar in the evening, and the next morning the plasmodium was found thus spread

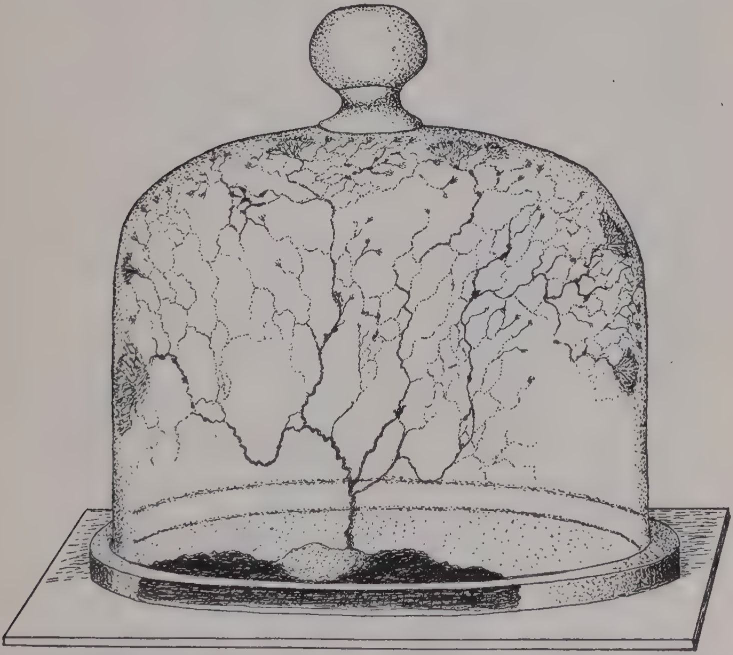

Fig. 65.—Plasmodium of a slime mould (Fuligo) spread over the inner surface of a bell jar from a piece of decaying wood; the result of 36 hours' growth. × ⅓.

out upon the glass in a very intricate, vein-like network. This illustrates the manner in which the plasmodium flows through the interstices of the decaying wood or other substratum. The plasmodium creeps by sending out extensions in various directions, and these extensions may anastomose to form a complicated network. Fig. 67, K represents a portion of the plasmodium enlarged. When observed in laboratory cultures the small plasmodia resemble in structure and movement a giant amoeba. Plasmodial masses twenty to thirty centimeters in diameter, and almost half a liter in volume, have been found on decaying apple pomace.

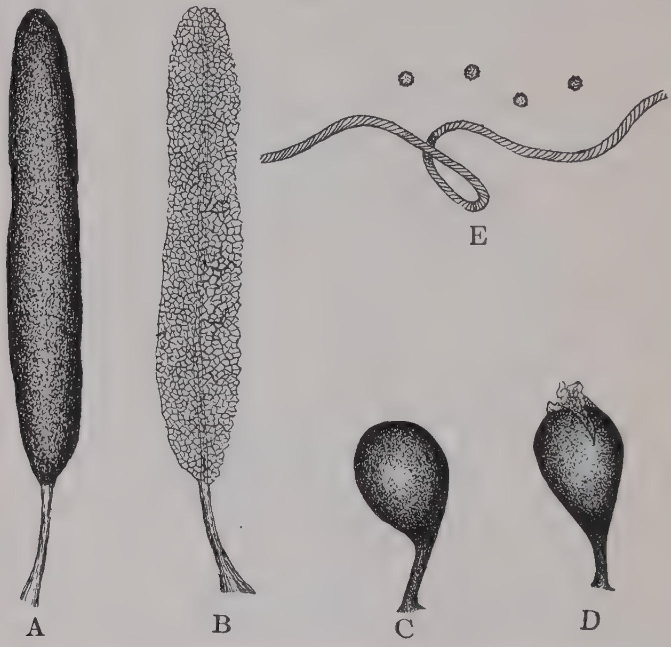

Fig. 66.—Individual sporangia of slime mould, greatly enlarged. A, B, *Stemonitis morgani* Peck. A, surface view; B, sporangium with spores dusted out, showing the fine netlike skeleton, the capillitium; the stalk, continued up through the capillitium, is known as the columella. C, D, E, *Hemitrichia clavata* (Pers.) Rost.; C, unopened; D, opened; E, spores and a piece of an elater.

With some exceptions, to be mentioned below, slime moulds are saprophytes; that is, they live on, and obtain their food from, *dead* organic matter.

Under certain conditions, as low temperature or lack of moisture, the plasmodium may pass into a dormant phase, forming a firm, dry lump of considerable size known as a *sclerotium*. These lumps may sometimes be divided into polyhedral masses, or cells, with cellulose walls. On the return of favorable conditions the cell walls will dissolve, and active growth will be resumed.

The Fruiting Phase.—As already mentioned, the fruiting phase involves the spore-bearing condition. When ready to produce spores, the plasmodium, which has thus far shunned the light, flows out of the interstices of the substratum into the light and collects into masses upon its surface, or creeps upon sticks, stones, or other objects lying upon the substratum, or upon the stems and leaves of plants, if the substratum be the soil. From these masses the spore-bearing bodies (sporangia) are formed. In species (Fuligo, Fig. 63 A) that live upon tan bark, decaying wood, or apple pomace, the spore-bearing structure is in the form of large cake-like masses. Figs. 64, A and 66, A, B, C, represent sporangia of common genera. Each sporangium consists of numerous spores held in a delicate network, the *capillitium*, which is not made of cells, but of dried and transformed protoplasm. Fig. 66, B shows the capillitium in Stemonitis after the spores have been dusted out. It consists of a thread-work supported by a slender stalk, the *columella*.

Life History.—Under the proper conditions of moisture and warmth, the spores* will germinate. They absorb moisture, increase in size, and as a result the walls break open. The contents of each spore escape as a swarm cell with one cilium, or, in certain species, as an amoeboid cell (Myxamoeba) (Fig. 67, A-E). The swarm cell moves about actively for a time, finally withdrawing the cilium and assuming the amoeboid form. The myxamoebae continue their amoeboid movement, increase in size, and divide (Fig. 67, F, G, H). The new

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* For our purpose a *spore* may be defined as a specially formed cell, which separates from the parent plant, and which by itself is capable of growth and division to form an individual.

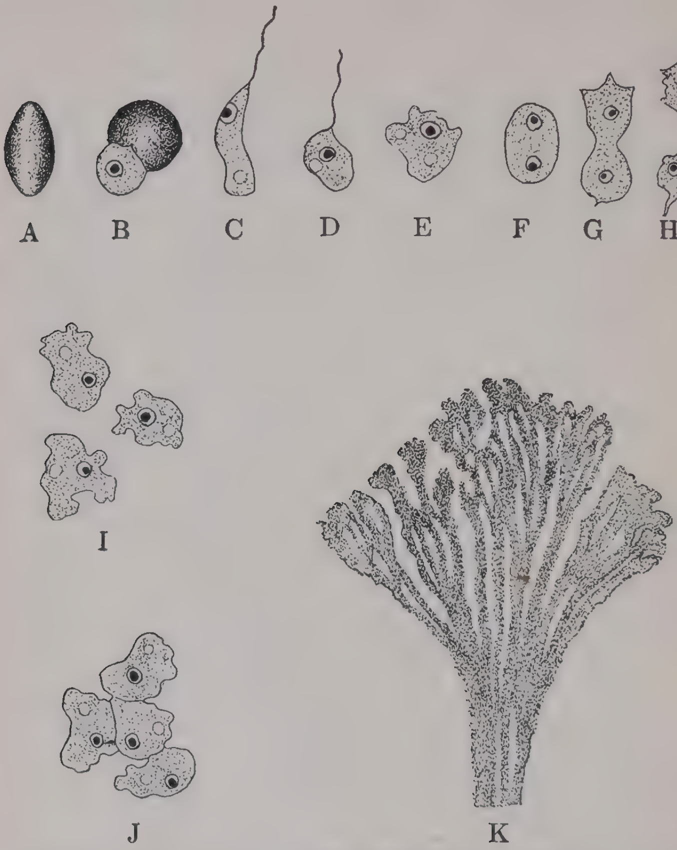

Fig. 67.—Development of the plasmodium from the spore. A to J, *Chondrioderma difforme*. A, spore; B, germinating spore; C, swarm cell; D, swarm cell changing to myxamoeba; F-H, division of myxamoebae; I, J, myxamoebae fusing; K, small terminal plasmodial fan from the plasmodium shown in Fig. 65. (A-E, I, and J, after Strasburger; F-H, after Brefeld.) × 500.

cells in turn grow and divide, division and growth continuing for some time, depending upon conditions of nutrition. The large number of myxamoebae finally unite into a common protoplasmic mass with many nuclei, the plasmodium (Fig. 67, I, J). In the formation of spores, the plasmodium by the process of division by surface cleavage furrows is broken up, first into larger multinucleated masses, which in turn give rise by continued cleavage into smaller and smaller masses, resulting finally in the minute uninucleated cells, each of which develops a cell wall and becomes a spore.

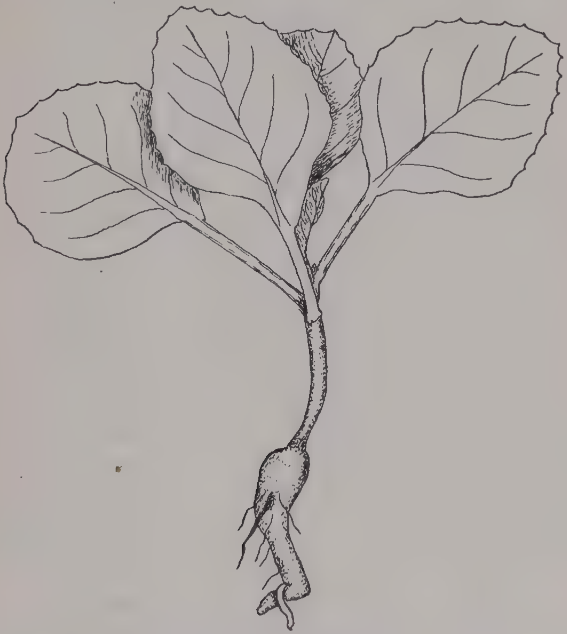

Fig. 68.—Seedling cabbage plant showing "club root" caused by the parasite, *Plasmodiophora brassicae* Woronin. × 1. (From Journal of Agricultural Research.)

The fusion of nuclei in pairs in the plasmodium of some species at a stage prior to the formation of spores has been reported by certain observers. This phenomenon is known as *karyogamy*, and it bears a resemblance to the fusion of nuclei in the union of gametes in higher plants.

Although nearly all of the 500 species of slime moulds are saprophytes, a few are parasitic upon higher plants. Among the latter, one species (*Plasmodiophora brassicae* Waronin) is parasitic upon the cabbage, causing the disease known as "club root" (Fig. 68). Another species (*Spongospora subterranea* (Wallr.) Johnson) produces "powdery scab" of the white or Irish potato.

FISSION PLANTS—SCHIZOPHYTA

The fission plants constitute a group of organisms of simple structure in which the fundamental distinguishing characteristic is the division of the cells by simple fission. This is the chief method of multiplication or propagation. In the majority of them, under certain conditions, special cells may be formed that function as spores, but these cells in many cases resemble the vegetative cells too closely to be regarded as typical spores. The individuals exist as single cells, colonies, or filaments. There are two groups of Schizophyta, the Cyanophyceae (Blue-Green Algae), which contain chlorophyll, and the Schizomycetes (Bacteria), which are devoid of chlorophyll.

BLUE-GREEN ALGAE—CYANOPHYCEAE

The Blue-Green Algae are distinguished in general by their blue-green color, which is due to the presence of the bluish pigment, *phycocyanin*, in the protoplasm along with chlorophyll. Phycocyanin is soluble in water. If a mass of the plants be dried and pulverized, to kill the cells, and placed in water, the blue coloring matter will be dissolved out. When the water is filtered off and the residue treated with alcohol, a greenish-yellow color will be dissolved in the alcohol, indicating the presence of chlorophyll.

It is of interest to note that not all Cyanophyceae are blue-green in appearance. Some are reddish, and some are yellowish.

The Cyanophyceae live both in fresh water and in the sea, sometimes occurring in such quantities as to impart their characteristic color to the water. The name Red Sea is said to have been given that body of water from the reddish hue imparted to the surface of the water by the presence of myriads of the blue-green alga, *Trichodesmium erythraeum.* Like many other lower plants they have an extremely variable habitat. They may be found upon moist earth, stones, or other objects, in ponds and streams containing decaying organic matter; in the roots of cycads and other seed plants; in the air spaces of aquatic ferns (Azolla); and within the bodies of certain liverworts. Some constitute the algal constituent of certain lichens (Collema, Peltigera).

Gleocapsa.—Let us now become better acquainted with the life of blue-green algae by the consideration of a few samples or type forms. One of the simplest is Gleocapsa. It exists as single cells or cell colonies* surrounded by a stratified, mucilaginous or jelly-like substance, as in Fig. 69, A, B, C. The stratified, gelatinous substance aids in distinguishing Gleocapsa from other unicellular blue-green algae. The gelatinous material is derived from the cell wall. The cell contents appear blue-green and densely granular. The pigments are located in the layer of cytoplasm next to the cell wall, and this layer is sometimes regarded as the chloroplast, which is in the form of a hollow sphere or cylinder.

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* A cell colony consists of two or more cells loosely held together. These cells may be alike in structure and potentially equal in function. Colonies may be indefinitely organized, that is, with the cells all alike and held together without any definite and fixed arrangement, or definitely and more highly organized, with the cells arranged in some rather definite and fixed pattern. In the latter case the cells may differ somewhat in structure.

Seldom in the Cyanophyceae do we find definite and sharply defined chloroplasts as in most plants containing chlorophyll. But in the genera Glaucocystis and Chrootheca well differentiated chloroplasts occur. The product of photosynthesis is said to be glycogen. In the cells of many of the blue-green algae, probably in Gleocapsa, there is in the center of the cell a body which is regarded as a nucleus (Fig. 69, D). In active vegetative cells the nucleus is usually found in some state of division, and for that reason a nuclear membrane, if present, might not always be observed. On the whole, it seems evident that the cell here is less highly specialized than in higher plants. The cell structure has been studied in but a few forms. Fig. 69, D is a stained section of a cell

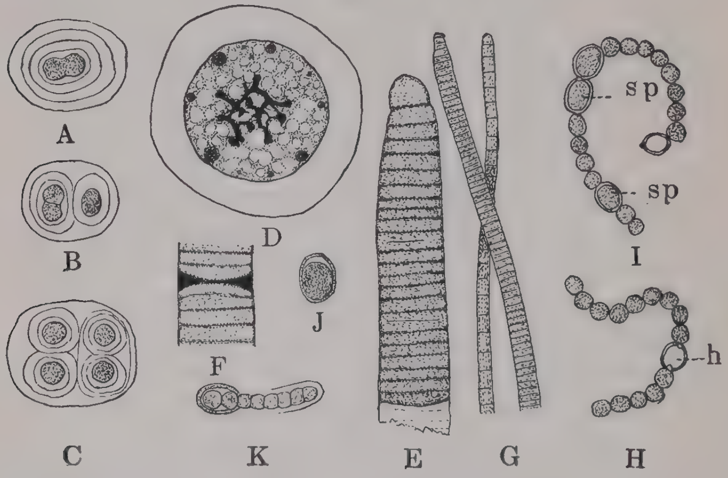

Fig. 69.—Blue-Green Algae. A-C, *Gleocapsa polydermatica*. A, a single cell, in which division has begun; B, two cells resulting from fission; the cell on the left is dividing; C, colony of four cells; D, fixed and stained cell of *Rivularia pisum*. The net-like central body represents the nucleus. × 3000. E, F, *Oscillatoria princeps* Vaucher. E, terminal portion of a filament; F, portion of a filament showing injured cell. × 540. G, a smaller species of Oscillatoria. H-K, Nostoc; H, portion of a filament; *h*, heterocyst; I, portion of vegetative filament with spores (*s*); J, spore; K, short filament produced by germinating spore. × 650. (A to C, after Strasburger; D, after Haupt; H, I, J, K, after Bornet.)

of Rivularia. The irregular structure in the center of the cell represents the nucleus; the dark round objects near the periphery represent glycogen granules. It is probable that the structure of Gleocapsa is similar to that of Rivularia.

Oscillatoria.—Oscillatoria is one of the simplest filamentous blue-green algae. It is common in ponds, streams, and moist places in which the water contains decaying organic matter. It forms floating masses or coatings or films on the earth or on objects under the water.

In the large species selected as an illustration (*O. princeps*) the cells are much broader than long, the filament resembling a row of coins placed with the flat sides together, as shown in Fig. 69, E. The cell structure is similar to that of Cleocapsa. The pigments are in a layer next to the cell wall, and this layer is in the form of a cylinder. Frequently granules of reserve material are to be seen arranged along the transverse walls. Each filament is surrounded by a sheath of gelatinous material, which, by swelling and expanding, helps to produce the progressive gliding or crawling movement so noticeable in species of this genus.

It is customary to speak of the filament as an individual. However, each filament may be looked upon as a colony of similar cells held together chiefly by the gelatinous sheath. If the filament be broken into pieces, or even into the individual cells, each uninjured cell or piece of filament will grow into a new filament. The filament has no definite base or apex. There may be some coöperation of the cells in the movement, and it is in the movement that the filament acts as an individual.

Nostoc.—A mass of Nostoc consists of filaments of beadlike, blue-green cells. At intervals in the filaments there are slightly larger, round, yellowish cells with thicker walls. These are the *heterocysts*, or limiting cells. As a rule they do not divide, and their function is unknown (Fig. 69, H, *h*). The gelatinous sheath of the filament is usually very thick, and the many sheaths together form the thick masses of jelly in which the plant is usually found. Sometimes in relatively pure water, these large, rounded masses, with uneven, lumpy surfaces, may attain the size of a lemon or small orange.

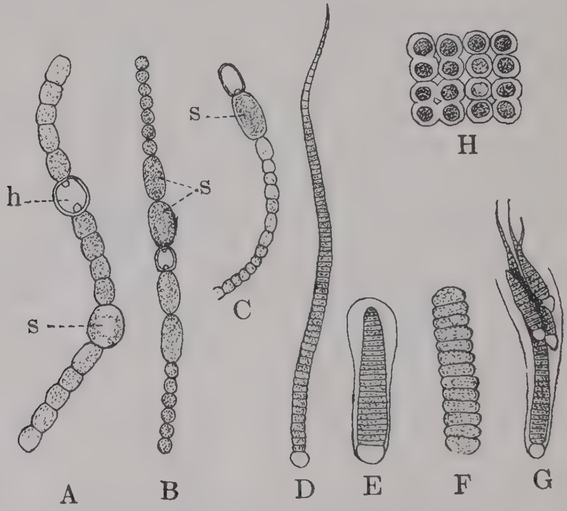

FIG. 70.—Blue-green Algea. A, *Anabaena azollae* Strasb.; B, *Anabaena inequalis* (Kutz) Born. and Flah.; C, *Cylindrospermum catenatum* Ralfs.; *h*, heterocyst; *s*, spore; D-G, *Rivularia bullata* Berk.; D, single filament; E, F, hormogonia; G, formation of hormogonium; H, Merismopedia. (A, C, from Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers. B, from "A Treatise on the British Freshwater Algae." By the late G. S. West; revised by F. E. Fritsch. Cambridge University Press, 1927. D–G, after Bornet, from Engler and Prantl.)

Anabaena.—Anabaena resembles Nostoc and is often found floating in water along with Nostoc (Fig. 70, A, B). It differs from Nostoc in that the filaments are usually straight and devoid of a sheath. They do not, therefore, form large, firm gelatinous masses, but a thin, mucus-like stratum. The heterocysts are numerous and generally distributed along in the filament. The spores are much larger than the vegetative cells. They may occur singly, or one on each side of the heterocyst, or, rarely, in continuous rows or chains. Certain species live in the intercellular spaces of the leaves of small floating aquatic ferns such as Azolla.

Cylindrospermum.—Cylindrospermum differs from Nostoc in that the filaments show some tendency to be differentiated into base and apex, and the cells are less rounded. Just above the heterocyst is formed a large spore (Fig. 70, C, *s*). Cylindrospermum does not form masses of jelly like those of Nostoc, but slimy films that spread over the surface.

Rivularia.—Rivularia forms globular or irregular masses of jelly in which the filaments are arranged somewhat radially. At the base of the filament is a heterocyst, above which a spore may be formed. The filaments end in long, slender, colorless cells. These filaments are differentiated, therefore, into base and apex, and contain three kinds of vegetative cells (Fig. 70, E).

Merismopedia is in the form of square or rectangular plates of cells, due to the regular division of cells in two planes at right angles to each other (Fig. 70, H).

Vegetative Propagation.—By vegetative propagation is meant the division or separation of any part of the plant to form another, or other individuals. If the plant be unicellular, the simple division of the cell accomplishes vegetative propagation; if multicellular, a separation of any vegetative part to become another individual constitutes vegetative propagation. With certain notable exceptions, almost all plants may be propagated vegetatively.

In the Cyanophyceae, vegetative propagation, which in some forms is the only method known, consists of simple fission of the cells. In certain filamentous forms there is another method, in which a piece of filament escapes from the gelatinous mass, moves away a short distance, and develops into another plant. Such pieces of filaments are called *hormogonia* (Fig. 70, E, F, G).

Propagation by Spores.—In some blue-green algae, as Nostoc, Cylindrospermum, Rivularia, and others, certain cells will develop a thick cell wall and pass into a dormant state, often losing their characteristic color. These are *spores*. On germination the spore develops, by growth and fission, into a plant like the one that produced it (Fig. 69, J, K). By means of spores the life of the plant may be tided over conditions unfavorable for vegetative growth. The spores are capable of living on dry land, and when dry may be scattered by the wind. The following diagram will indicate graphically the two methods of propagation:

By fission:	By spores:
Plant	Plant
↓	↓
Plant	Spore
↓	↓
Plant	Plant

BACTERIA—SCHIZOMYCETES

Bacteria are unicellular fission plants devoid of chlorophyll, hence called *Schizomycetes* (fission fungi). With some notable exceptions they are either parasites or saprophytes. They are among the simplest and smallest of all living things, some of the globular forms being less than one micron (1/25,000 inch) in diameter. Individual bacteria appear colorless, but, in large colonies or masses, various species exhibit bright and characteristic colors. For example, one species growing on bread (*Micrococcus prodigious*) forms blood-red specks or patches. Those which exhibit colors in this way are called *chromogenic* bacteria.

The form of the cell in some bacteria is globular, and these are designated by the collective term *cocci*,* as Micrococcus, Staphylococcus, etc. Those in the form of straight rods belong generally to the genus Bacterium, if non-motile, and to Bacillus (Migula) if motile.† Rod-shaped forms with a slight spiral curve are called Vibrio, and those more strongly curved, Spirillum. Certain straight filamentous forms are termed Leptothrix and the spirally wound filaments, Spirochaete.

Many bacteria are actively motile, due to the presence of one or more cilia, which may be borne at one or both ends, or distributed over the entire surface of the cell. Some bacteria, as the hay bacillus (*Bacillus subtilis*) are motile in certain stages of their life-history and non-motile in other stages. Spores are never motile. Several forms of bacteria are shown in Fig. 71.

Bacteria live as isolated cells or in the form of films or masses, known as *zoöglea*. One of the most remarkable zoöglea-forming species is *Leuconostoc mesenterioides* (Cienkowsky) Van Tieghem, which gives rise to the large gelatinous masses formerly known as "frog-spawn" or "gomme du sucrérie" in European sugar factories. The plant consists of Nostoc-like colonies of rounded cells embedded in a gelatinous substance (Fig. 71, C). The individual colonies form rounded or elongated masses of about two cubic centimeters in volume, but so rapid is growth under favorable conditions that a volume of 4900 liters of 10% sugar solution may be converted into a gelatinous mass in 24 hours.

Each cell is provided with a definite cell wall, which in rare instances shows a cellulose reaction (*Bacterium pasteurianum*). As regards the internal structure of the cell little is known, owing to the fact that the contents stain uniformly throughout. The presumption is in favor of a nucleus in each cell, but nothing is known concerning the details of such a body. Several forms of bacteria are illustrated in Fig. 71, A-J.

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* Coccus, pronounced cok′kus; but cocci, cok′si.

† Erwin Smith included in the genus Bacterium non-motile rod-shaped forms and those possessing cilia at the end. Those that bear cilia scattered over the cell are placed in the genus Bacillus.

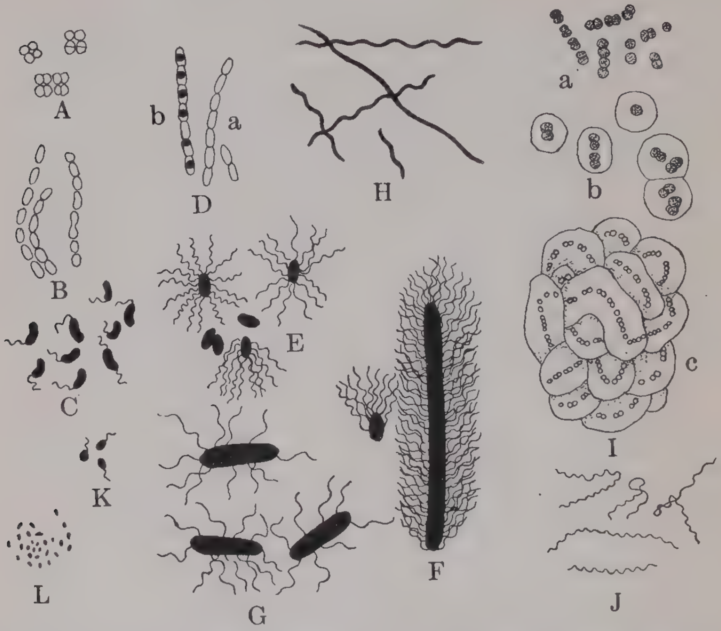

Fig. 71.—Various kinds of bacteria. A, *Micrococcus scarlatinus* Mig.; B, *Bacterium aceti* (Kutz.) Zopf., acetic acid bacteria; C, *Microspira comma* (Koch) Schröter, cholera bacterium; D, *Bacillus anthracis* Koch, × 1500; E, *Bacillus typhi* Gaffy, typhoid bacteria; F, *Bacillus vulgaris* (Hauser) Mig.; G, *Bacillus subtilis* (Ehrenb.) Cohn, hay bacillus; H, *Spirrilum tenue* Ehrenb.; I, *Leuconostoc mesenteriodes* Cienk. (*Streptococcus mesenterioides* (Cienk.) Mig.); *a*, in sugar free culture; cells not surrounded by gelatinous substance; *b*, cells surrounded by gelatinous substance; grown in sugar-containing medium; *c*, older gelatinous mass; J, *Spirochaeta obermeiri* Cohn; K, *Nitrosomonas europea* Winogradsky) Mig., nitrate bacteria. All except D, × 1000. (A, after Migula; B, C, E, F, G, H, J, from Engler and Prantl; D, I, K, L, after A. Fischer.)

Vegetative Propagation.—The chief method of propagation in all bacteria is vegetative, consisting of the simple fission of the cell at the middle. Under certain favorable conditions many bacteria multiply rapidly, a division being accomplished in about half an hour. It will be seen that, under such circumstances, the descendants of an individual may amount to millions in a period of 24 hours.

Propagation by Spores.—All, or nearly all, bacteria produce what are known as spores, and two forms of spores are recognized. In the one case the cell contents contract and develop a new thick wall within the parent cell (Fig. 71, D, *b*). These are internal, or *endospores*. On the other hand, the cell may merely thicken its wall, forming what is known as an *arthrospore*. Spores are formed presumably when conditions become unfavorable for vegetative activity, and the plant is thus tided over such conditions. Spores of bacteria are very resistant, some being able to withstand the temperature of boiling water for half an hour or longer.

Distribution.—Bacteria occur in every region of the earth that is capable of sustaining life of any kind. Many live within the tissues of plants and animals, where their presence may produce the abnormal condition known as disease. Although most bacteria require the oxygen of the air (aerobic bacteria), many, like those that live in the mud under water or at the bottom of a pond, and those causing such diseases as tetanus (lockjaw), thrive in the absence of oxygen. In fact, some are unable to develop in the presence of air; such bacteria are said to be *anaerobic*.

Bacteria in the Economy of Nature and of Man.—Inasmuch as many bacteria are harmful to plants, lower animals, and man, there is a widely-prevailing popular notion that all bacteria are injurious. But, as a matter of fact, these small plants are among the most useful and necessary organisms. If all bacteria were to perish from the earth, the balance of nature would be so upset that the result cannot be imagined. In past ages these plants played a part in the formation of various geological deposits. In the soil their activity is such that, though at present very imperfectly understood, doubtless many higher plants could not thrive if bacteria were absent. By their activities (fermentation and decay) the waste products and dead bodies of plants and animals are converted into the elementary compounds out of which these plants and animals were composed. Bacteria not only contribute to the renewal of the soil, but also render it suitable for use by higher plants. Certain bacterial fermentations are the means by which many foods are produced for the use of man and animals.

Let us now turn our attention to a few of the kinds of bacterial activity.

Nitrifying Bacteria.—Certain bacteria living in the soil, though devoid of chlorophyll, secure their food from purely inorganic material. One of these (Nitrosomonas) oxidizes ammonia to nitrous acid. Another (Nitrobacter) oxidizes nitrous acid to nitric acid. Nitric acid thus produced may then combine with other substances in the soil, forming soluble nitrates useful to plants. The work done by these bacteria is referred to as chemosynthesis.

Nitrogen-fixing Bacteria.—Certain other bacteria found in the soil (*Bacterium leguminosum*) enter the roots of leguminous plants, chiefly through the root hairs, and cause the formation of nodules or tubercles (Fig. 72). These bacteria are able to assimilate the free nitrogen of the air. Let it be distinctly understood that most plants cannot utilize the free nitrogen of the air. It must first be converted into nitrates. While the air is extremely rich in nitrogen (nearly 80% by volume), the soil beneath it may contain very small quantities of nitrates, or almost none. The relation of these bacteria to a bean or clover plant, for example, is as follows: The bacteria gain entrance to the cells of the cortex of the root. Here they live and multiply, at first as parasites upon the root cells. Their presence in the root stimulates the latter to an over-development (hypertrophy) in the parts occupied by the bacteria, resulting in the gall or tumor-like growth called a *nodule* or *tubercle*. By the time the nodule has reached its definite size, the bacteria have become large and rich in protoplasm. At this point the roots of the plant begin to digest and assimilate the bacteria, which are rich in nitrogenous material. The bacteria are, therefore, the intermediary through which the bean or clover secures

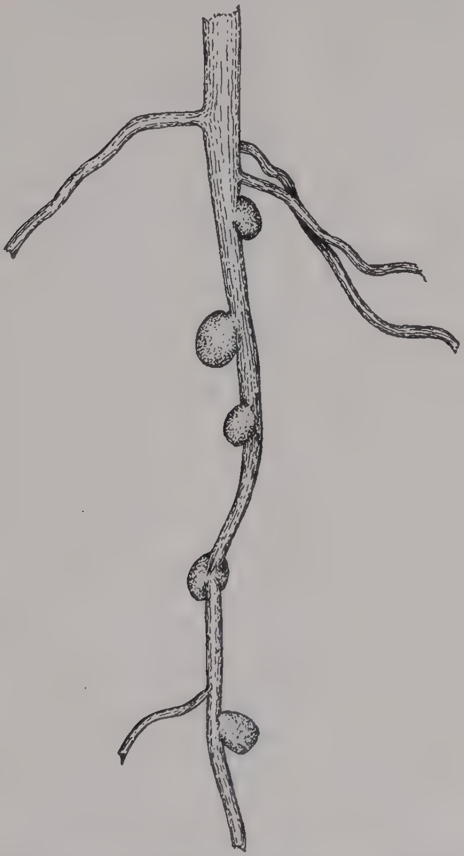

Fig. 72.—Root of clover with tubercles (galls) due to infection by bacteria (*Bacterium leguminosum*).

nitrogen. If these bacteria are present in the soil, such plants as beans, clovers, etc. will thrive, although the soil is exceedingly poor in nitrates. The soil is left much richer in nitrates after the growth of such leguminous plants. If the bacteria are not present in the soil to begin with, they may be grown in laboratory cultures and scattered over the ground in which the leguminous plant is to be grown. The soil may also be inoculated by scattering over it a quantity of soil from a field in which the proper leguminous plants have recently grown.

Iron Bacteria.—A few bacteria (*Cladothrix dichotoma*, *Leptothrix ochracea* Kuntzig, *Spirophyllum ferrugineum* Ellis, *Gallionella ferruginea* Ehren.) are able to utilize iron salts, and, as a result, iron oxide is deposited in a sheath formed by the cell wall. The surface of water may sometimes appear rusty red, owing to the presence of these bacteria.

Sulphur Bacteria.—Bacteria that utilize compounds of sulphur are more abundant than iron bacteria. They oxidize hydrogen sulphide, the sulphur being set free in the form of granules in the cell. Some sulphur bacteria are colorless (*Beggiatoa alba*), while certain others (*Cromatium Weissii*, *Thiocystis violacea*) possess a violet or purplish pigment, *bacterio-purpurin.*

Sulphur and iron bacteria have doubtless played an important role in past ages in the formation of such geological deposits as kaolin. There is also some evidence to indicate that certain bacteria as *Micrococcus silenicus* Brenner, which occur in mud or ooze under water, are capable of oxidizing silenium, although that fact has not as yet been definitely established. Such bacteria are sometimes regarded as representing a more primitive type of organism in which metabolism is simpler. It would seem probable that a number of exothermic reactions which take place in ooze play a role in the maintenance of life in such organisms.

Bacteria which secure their sustenance or energy largely from inorganic matters are said to be *autotrophic.*

Pathogenic, or Disease-producing, Bacteria.—We shall here call attention to a few bacterial diseases of plants only. All of our knowledge of bacterial diseases of plants began about 40 years ago, when T. J. Burrill demonstrated that the common fire-blight of pear, apple, and quince was caused by the parasite, *Bacillus amylovorus* (T. J. Burrill) Trevison. Sixteen years later Erwin F. Smith ventured the statement that "there are probably as many bacterial diseases of plants as of animals," and more recently the same author offered an even broader generalization, namely, that in all probability it will be found that bacterial diseases occur in every family of plants.

In the body or cells of the host, the bacteria produce poisons (toxins) and may kill or disorganize the cells. The whole plant may be affected, or the effect may be local and confined to some particular part.

The fire-blight of apples, pears, and quinces kills young shoots and sometimes the larger branches, causing the leaves to turn brown as if scorched by fire. Infection is brought about by bees and other nectar-sipping insects, which carry the bacteria from "hold-over blight" or "cankers" of previously diseased trees to the flowers, where the organism begins its growth in the nectaries. From the blossoms it passes down, mainly through the bark, into the larger branches of the trunk. The destruction of the cells of the inner bark girdles the branch and causes its death.

Crown gall, plant cancer, is due to the parasite, *Bacterium tumefaciens* Smith and Townsend. The presence of this organism in the host tissue results in an overgrowth of the affected part (Fig. 73). This, usually large, tumor or knot-like growth often occurs on the trunks of fruit trees near the ground, that part

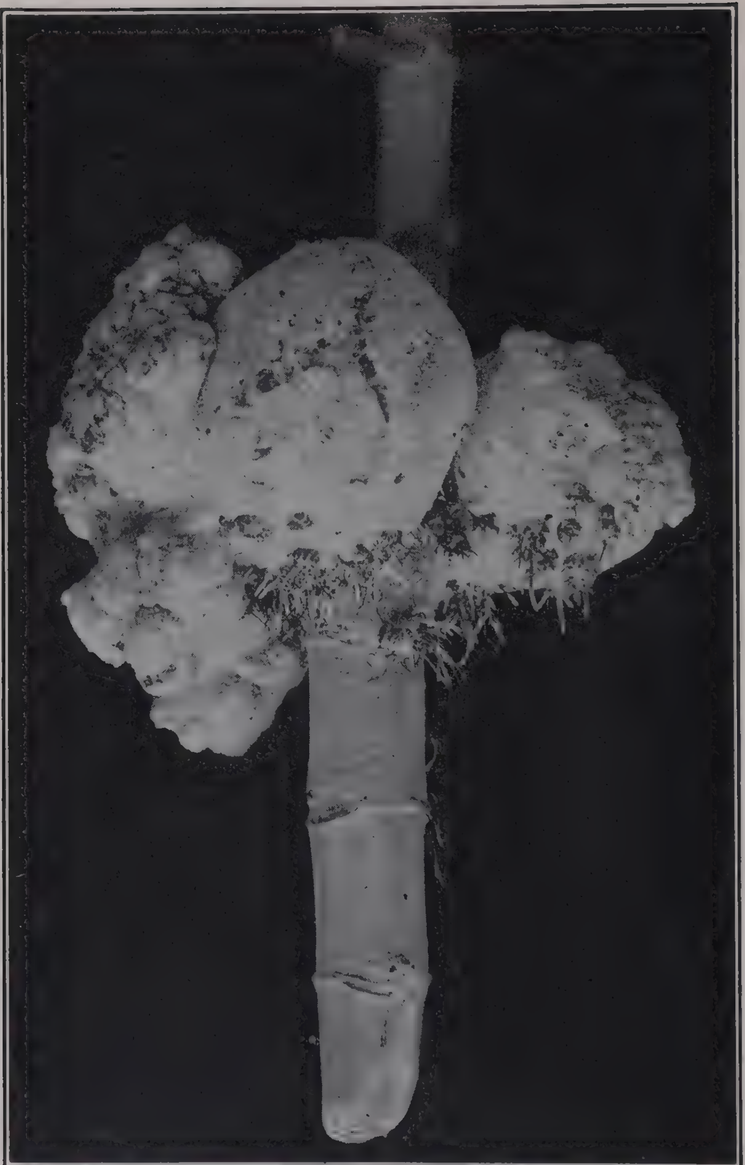

FIG. 73.—Crown gall or tumor-like proliferations of the stem of *Bryophyllium calycinum* inoculated with *Bacterium tumefaciens* (hop strain). Photo by the late Erwin F. Smith.

known by gardeners as the "crown." The disease occurs on a great variety of cultivated plants, and upon some wild ones, as the chestnut. The cells of the parts affected are not killed or destroyed, but are stimulated to abnormal growth and division, the result being a gall that may be larger than the root or stem that bears it. In this behavior of the cells of the host, crown gall bears a striking resemblance to human cancer. The largest galls develop from the cambium, but smaller ones may be formed from the bark. Fruit trees may live and bear fruit several years after the noticeable presence of the gall.

Cucurbit, or Cucumber, Wilt is caused by *Bacillus tracheiphilus* E.F.S. It occurs upon various members of the cucumber family, but is it not known outside of this family. The bacteria grow inside the conducting vessels of the xylem, producing a slime or mucilage that plugs the vessels. This prevents the passage of sufficient water to the leaves, thereby causing them to wilt. The leaves wilt suddenly, and without apparent cause, and the whole plant dies in a short time. Infection is spread by certain insects that feed upon the plants.

Brown Rot of the Solanaceae results in the wilting and rotting of leaves and stems. It is caused by *Bacterium solanacearum* E.F.S. It occurs on potato, tomato, egg plant, and other members of the nightshade family, as well as upon species of the nettle and bean families.

Among other common bacterial diseases are the black rot, or "black leg," of potato, due to *Bacillus phytophthorus* Otto Appel; the bean blight caused by *Bacterium Phaseoli* E.F.S.; mulberry blight caused by *Bacterium Mori* Bayer and Lambert emend. E.F.S.; and others too numerous to mention here.

Bacterial parasites act variously upon the plant. Sometimes the plant as a whole is affected, resulting in an early death; or the disease may be confined to certain circumscribed portions. On the other hand, parasitic bacteria may produce no injury to the plant as a whole, but may be even beneficial, as in the case of the tubercle bacteria of the legumes, where the relation is regarded as one of mutual symbiosis. One of the most remarkable cases of mutualism is found in the tropical East Indian Ardisia, a hothouse plant grown for its ornamental red berries and evergreen foliage. The bacteria are most abundant in the leaf teeth, where they form pockets or cavities, making the teeth appear yellow and swollen, but never causing the leaves to die or fall. Plants grown from seeds in the absence of bacteria remain very small and stunted. It would thus seem that Ardisia requires the bacteria.

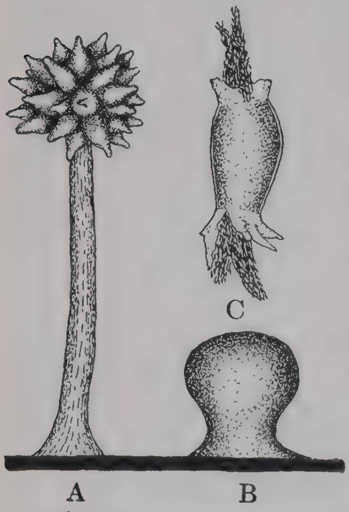

Fig. 74.—*Chondriomyces apiculatus* Thaxter. A, cystophore with cysts in different stages of development; B, young cystophore; C, cyst germinating. On dung of antelope, from Liberia, Africa. (After Thaxter.)

MYXOBACTERIACEÆ

The Myxobacteriaceae consist of bacteria-like cells held together by a slimy or mucilaginous substance which they secrete, thus forming a pseudo-plasmodium that bears some resemblance to the plasmodium of the slime moulds. It differs from the latter, however, in that the cells do not fuse. The cells bear a close resemblance to round or rod-shaped bacteria, and exhibit a slow, creeping movement. After the vegetative period, which, in artificial cultures, may last a week or two, very definitely-shaped and bright-colored fructifications are produced in some species, as shown in Fig. 74, A. Here we have a little column or stalk, at the top of which are formed the pear-shaped cysts (sporangia) containing the spores. The wall of both cyst and stalk is formed from the hardened mucilaginous material. The germinating cysts give rise to new pseudoplasmodia (Fig. 74, C). Nearly all the members of this group live saprophytically upon the dung of animals. Almost our entire knowledge of this interesting group of plants is due to the researches of Thaxter.

CHAPTER XI

CHLOROPHYCEAE, GREEN ALGAE

CONJUGALES. POND OR WATER SILKS AND DESMIDS

The Conjugales include those algae commonly known as pond silks or water silks. They occur only in fresh water. The individual plants are either single cells or filaments. They are recognized by the characteristic chloroplasts, which may be in the form of a band, or a number of bands, spirally arranged in the cell, a flat plate, or a star-shaped body.

Spirogyra.—As an introduction to the study of the green algae we may select as a concrete illustration the very familiar Spirogyra, inasmuch as some first-hand knowledge of the plant may be acquired by the beginner in his laboratory exercises.

Spirogyra is an unbranched filament, consisting of a single row of cylindrical cells placed end to end. The cells secrete a slime, making the mass of filaments slippery to the touch. Each cell may contain one or more band-like chloroplasts—the number depending largely upon the species—arranged spirally in the cell (Fig. 75, *a*, *c*). The band-shaped chloroplasts usually have irregular or scalloped edges, and they are not always flat, but may be trough-shaped. Spaced at regular intervals in the chloroplasts are *pyrenoids*, conspicuous bodies that are centers for the formation of starch (Fig. 75, A, *p*). The bulk of the cytoplasm in the cell forms a layer on the inner surface of the wall, and in this the spiral chloroplasts are held. The center of the cell is occupied by a large vacuole containing cell sap. In this the nucleus is suspended in a mass of cytoplasm, from which radiate strands of cytoplasm which end in the pyrenoids or the wall layer of cytoplasm (Fig. 75, A, *n*).

The cell wall is thin and colorless. Upon it is produced externally the mucilaginous slime. The end walls of the cells in some species show characteristic infoldings.

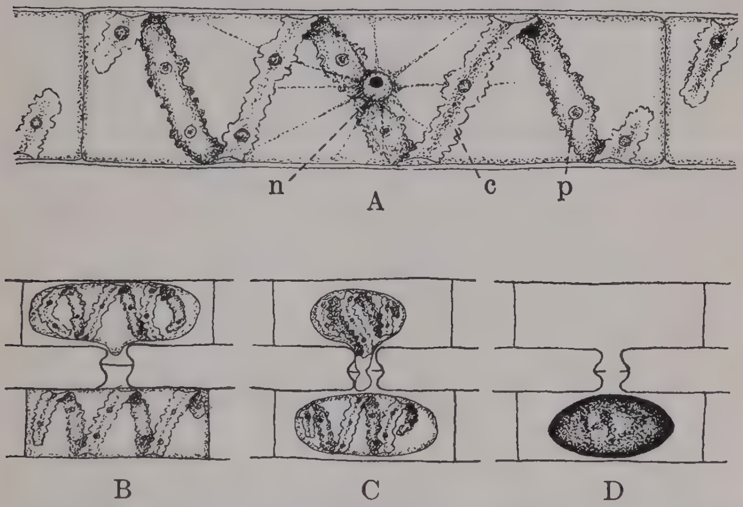

Fig. 75.—Spirogyra. A, a vegetative cell; *n*, nucleus with its radiating strands of cytoplasm; *c*, chloroplast; *p*, pyrenoid. B-D, formation of zygote.

Vegetative Propagation.—The cells of Spirogyra multiply by transverse division. Normally cell division occurs at night, beginning about nine o'clock or later. In order to observe the division in daylight it is necessary to inhibit the process by lowering the temperature at about the time division begins, and keeping the specimens at the low temperature until the time of observation the following day.

The filaments of Spirogyra may break into two or more pieces, and each piece may, by the growth and division of its cells, develop into a longer filament. If filaments are transferred from their normal habitat out of doors to a laboratory vessel, they undergo disintegration, as a rule, many of the cells dying. The parts that remain alive, occurring as single cells or as short pieces of filaments, may grow into new filaments after a time, thus restocking the vessel. With few exceptions there is no asexual propagation in the Conjugales by means of spores. Occasionally the contents of certain cells will round up to form a cell resembling a spore, which is termed an *aplanaspore*. Aplanaspores probably represent only a form of vegatative propagation.

Sexual Reproduction.—In Indiana Spirogyra reproduces sexually in the open during March and April, although fruiting specimens may be found during the summer and in the autumn.

Two filaments, or parts of filaments, parallel each other close together, often becoming twisted about each other if they are of considerable length. The opposite cells of the filaments send out short protuberances, which meet end to end, and a conjugating canal results from the dissolution of the walls. This dissolution is effected by a cellulose-dissolving enzyme produced by the protoplasm. In one of the filaments, as a rule, the contents of the cells will become self-plasmolyzed, thus rounding up and separating from the cell wall, but remaining in the cell cavity. These are called receiving cells (Fig. 75, C). The cells of the other filament will likewise become self-plasmolyzed. The protoplasm of the cells of this filament will, however, not remain within the parent cell walls, but will move through the openings into the opposite cells, as in Fig. 75, C, D, where the contents of the two cells will fuse, forming one cell. The two nuclei will also fuse (Fig. 76, A). The cell whose protoplast moves over into the receiving cell is termed the supplying cell. The supplying cell usually rounds up before the self-plasmolysis of its receiving mate.

The protoplasts of the two cells that unite as described, are called *gametes* (sex cells). The supplying protoplasts are known as male gametes, and the filament as the male plant, while the receiving gamete is the female gamete, and the filament is the female plant.

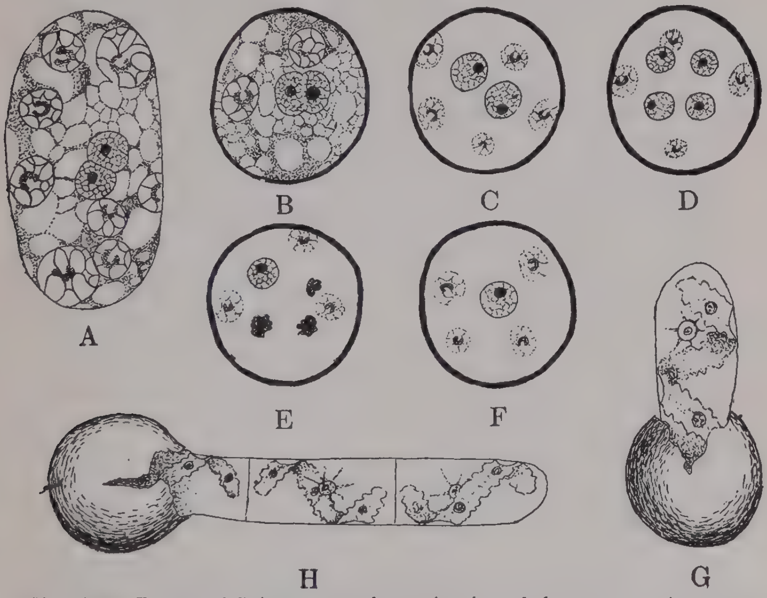

Fig. 76.—Zygote of Spirogyra, and germination of the zygote. A, young zygote with the two gamete nuclei in contact. B, zygote after fusion of gamete nuclei and formation of the thick wall. C-F, stages preparatory to the germination of the zygote; C, after first nuclear division; D, after division of the daughter nuclei; E, three nuclei degenerating; F, zygote just before the bursting of the wall. G, H, young filaments developing from the zygote. (A and B from Mottier, Fecundation in Plants; D to H diagrammatic.)

The new cell formed by the union of the two gametes is termed a zygote (Fig. 75, D). When the contents of the two cells fuse, the nuclei are seen lying in contact (Fig. 76, A, B). Later they fuse completely. In Fig. 76, B, the fusion is almost completed, and the resulting zygote develops a thick cell wall composed of three layers. The exact behavior of the chloroplasts in the zygote is not well understood. The new plant which develops from the zygote will have the same number of chloroplasts as either parent, but not twice as many. The zygote develops a thick cell wall, and the contents assume a dark color. It now passes into the resting stage, or period of dormancy, and, in this condition, the zygote may retain its viability for some months on dry earth.

In some species of Spirogyra the adjacent cells of a single filament conjugate to form a zygote.

Germination of the Zygote.—On the return of moisture and other favorable conditions the zygote will germinate. With the increase in size, due to absorption of water, the two outer layers of the cell wall are ruptured, and the young plant with the inner layer as its wall emerges as an elongated cell (Fig. 76, G). This divides transversely into two cells. The more slender basal cell becomes the holdfast, if the plant is to become attached to some support, and the terminal cell continues growth and division. Unless the filaments are attached to some object in the water, Spirogyra does not manifest a differentiation into base and apex. The basal cell may not divide, but the terminal cell elongates and divides, and the resulting cells in turn repeat the process. In this manner a new filament of indefinite length may be produced.

Haploid and Diploid Structure.—We may now inquire a little more fully into the significance of the union of gametes, or sexual reproduction. By the term *gamete* we mean a specially formed cell, which alone is incapable of growth and division to form an individual, but which is capable of uniting with another similarly formed cell, presumably of a different sex, also called a gamete. The product of the union, namely the zygote, is then capable of growth into a new individual.

We have learned in a preceding chapter (page 5) that each dividing nucleus reveals a certain number of chromosomes. Each gamete nucleus, let us say, contains the single (*haploid*) number of chromosomes. When the two gametes fuse, the fusion nucleus possesses twice the number of chromosomes, or the double (*diploid*) number. The zygote of Spirogyra contains the double number of chromosomes. It is, therefore, the diploid condition, or *diploid structure*. Unless some profound change took place, the gametes of the next generation would contain the double number, and the zygote four times the single number of chromosomes. It is evident that after a few generations the number of chromosomes would become very great. But, as a matter of fact, the new plant coming from the zygote does not possess the double, or diploid, number of chromosomes, but only the single, or haploid, number. A very profound change must have taken place during the germination of the zygote, by which the double number of chromosomes in the nucleus gave way to the single number.

In the zygote here under consideration, the double number of chromosomes in the nucleus resulted from a *union* of the two nuclei of the gametes, each contributing an equal number. The only way known by which the number of chromosomes in a nucleus can be reduced is by a process of nuclear division called a *reduction division*, or *meiosis*. With the aid of Fig. 77, we shall see what happens to the chromosomes during a reduction division of the nucleus. Let it be understood that the illustrations of this figure are merely diagrams of a few stages of the process; they are not pictures of the actual steps that would be seen in Spirogyra or in any other plant.

In the reduction division a spirem is formed as in the case of an equational division. Fig. 77, A, corresponds to the stage of the spirem, which represents all the chromosomes united end to end. In this case there are six, but the limits of any chromosome are not recognizable. The spirem now segments into the six chromosomes, which tend to be arranged in pairs, as in B. The three pairs are next arranged on the spindle, as in C. Now, one member of each pair passes to one pole of the spindle, and the other member to the other pole, as in D. Each daughter nucleus (E) thus formed receives three chromosomes of the six, or just one-half the number possessed by the parent nucleus. The nuclei of these two cells are, therefore, haploid nuclei.

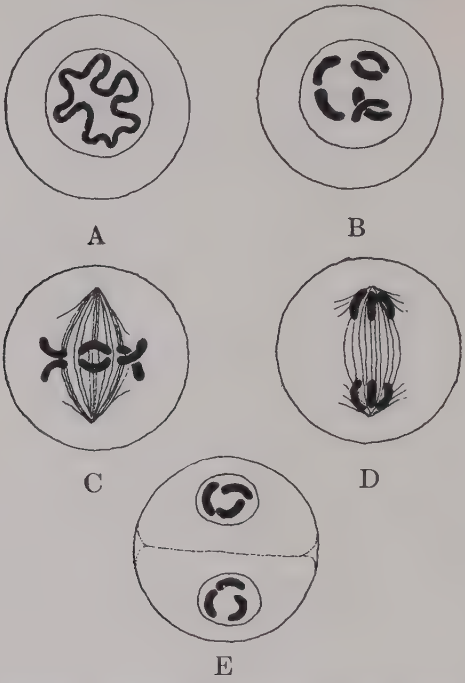

Fig. 77.—Diagrams illustrating a reducing nuclear division. A, the hollow spirem. B, spirem has segmented crosswise into the chromosomes which have approximated in pairs. C, pairs of chromosomes arranged in the equator of the spindle. D, one of each pair, or one-half the whole number, has reached the pole of the spindle. E, daughter nuclei, each with the reduced number of chromosomes.

The nuclear history from the fusion of the gamete nuclei to the germination of the zygote in Spirogyra is as follows: The nucleus resulting from the fusion of the two gamete nuclei divides (Fig. 76, C). The two resulting nuclei divide also, giving rise to four nuclei (Fig. 76, D). Of these four nuclei, three disorganize, and the remaining one functions as the nucleus of the new plant, which has the haploid number of chromosomes (Fig. 76, E, F). The reduction of the number of chromosomes to one-half, or the change from the double number to the single number, took place in the first of these two nuclear divisions.

Now, it is a well established fact that in all plants which reproduce sexually there are two structures or conditions in every life cycle. All those cells of the same life cycle whose nuclei contain the double (diploid) number of chromosomes make up the diploid condition or structure. The union of gametes, therefore, marks the beginning of the diploid structure or condition, and the reduction division following union, whenever or wherever it occurs, ushers in the beginning of the haploid structure. These two structures follow each other in alternate succession in every life cycle involving sex. In Spirogyra the zygote represents the diploid structure, and the cells of the filament, the haploid structure.

As we proceed in our study of different plant groups, from the lower to the higher, we shall find that the haploid and diploid structures differ in various ways as regards size, appearance, and physiological dependence one upon the other. In some plants the diploid structure is dependent upon the haploid, the two being anatomically one plant; in other groups the reverse is true, namely, the haploid structure being dependent upon the diploid. In still other plants the haploid and diploid structures represent two very distinct and easily recognizable individuals or plants, which may become entirely independent, attaining a different size and structure, and varying greatly in the length of their lives.

The great outstanding and significant function of sex-reproduction in the realm of living organisms is the *creation of the diploid structure*, for the highest and most important part of the highest animals and plants is the diploid structure. The evolution of the highest forms of life that we know seems to have been possible only through the instrumentality of the diploid structure.

Hydrophyte, Xerophyte, and Mesophyte.—Plants that live in water or in marshy places are called *hydrophytes*, when mentioned with reference to their physical environment. In the vegetative condition, then, Spirogyra would be a hydrophyte, or an aquatic plant. Plants such as cacti, that may live where there is a minimum of water, as in a desert, are known as *xerophytes*. Plants such as our forest trees of beech and maple, and the ordinary flowers and ferns that grow among them, as well as ordinary crops, requiring intermediate conditions of moisture supply and drainage, are called *mesophytes*, or middle plants. A mesophyte or a hydrophyte may take on a *xerophytic condition* and exist with only a very limited water supply, as in the case of our deciduous forest trees in winter. A beech tree, for example, is not a xerophyte, but in the winter it is in a xerophytic condition.

The zygote or Spirogyra will remain viable when the pond dries up, and the bottom of a dried-up pond represents a xerophytic environment in so far as Spirogyra is concerned. The zygote is therefore, the dry land stage of the otherwise aquatic plant. It is thus seen that it is the zygote in Spirogyra that enables the plant to tide over conditions unfavorable or unfit for its vegetative development.

Zygnemaceae. Pond Silks.—In our flora the majority of the Conjugales belong to the Zygnemaceae and the Desmidiaceae, Desmids. Of the Zygnemaceae the genera most commonly met with in our local flora are

Spirogyra, Zygnema, and Mougeotia (Mesocarpus). All of these consist of unbranched filaments. In Zygnema there are two star-shaped chloroplasts in each cell, while the cells of Mougeotia contain each a long chloroplast that appears as a straight, flat band, or it may have a twist at the middle. All of these plants when not attached to objects below the surface of the water may form floating masses, which are buoyed up by entangled bubbles of gas derived from the process of photosynthesis and the expansion of air in the water.

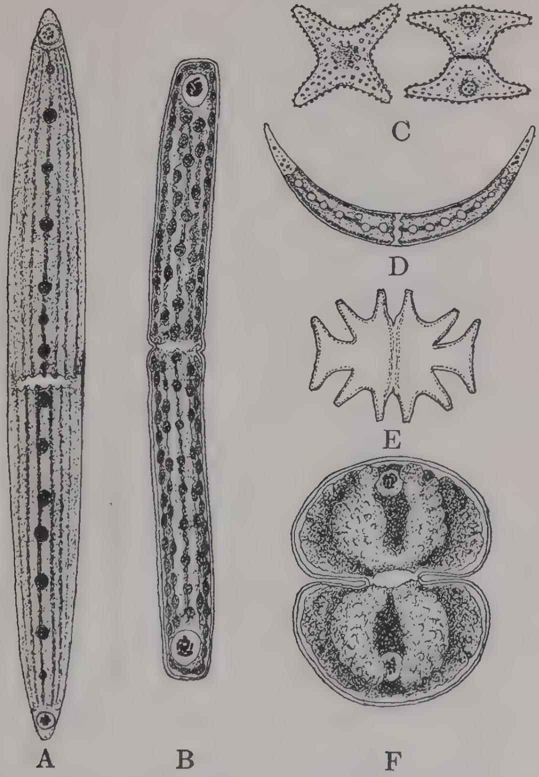

FIG. 78.—Some common Desmids. A, D, Closterium; B, Docidium; C, End and side views of Staurastrum; E, Micrasterias; F, Cosmarium. (E, after Wolle.)

Desmidiaceae, Desmids.—Desmids are unicellular plants that live as isolated cells, or the cells may adhere to form filaments. The numerous species are all confined to fresh water. Many are objects of beauty because of their form and symmetry. Most desmids consist of two symmetrical halves with the nucleus near the center of the cell (Fig. 78, A to F). The chloroplasts, as in other Conjugales, are always in the form of some definite pattern, one or two to each cell. The chloroplasts may be star-shaped, lobed, or in the form of flattened, radiating plates united in the axis of the cell. One or more conspicuous pyrenoids are present in the chloroplasts of some species. In forms like Closterium and Docidium (Fig. 78, A, B, D) a vacuole is usually present in each end of the cell, in which are seen minute crystals of sulphate of lime in active movement. This kind of movement is known as a Brownian movement, named in honor of the discoverer, Robert Brown.* Fig. 78, A-F, represents some of the commoner forms of desmids met with among the filamentous conjugales or along with other algae.

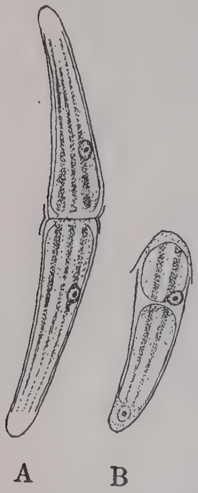

Fig. 79.—Vegetative propagation in the Desmid, Closterium. A, the cell has just divided; B, one of the old half-cells regenerating a new half. The chloroplast of the old half-cell has divided, and the nucleus is taking position between the two plastids. (After A. Fischer.)

Vegetative Propagation.—Desmids propagate vegetatively by a transverse division at the middle of the cell (Fig. 79, A, B). After the division of the cell each half develops a new half cell. Consequently, each resulting desmid consists of one old half and a newly regenerated half (Fig. 79, B). The chloroplast for the new half-cell grows out from that in the old half-cell.

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* Discovery reported in 1827.

Sexual Reproduction.—The process of the formation of the zygote may be illustrated in the well known Closterium or Cosmarium. The two cells approach each other and are held together by the mucilaginous slime. Each cell sends out a protuberance. These meet end-to-end and form a conjugating canal as in the case of Spirogyra. The two protoplasts, however, meet in this canal, and there fuse to form the zygote (Fig. 80, A to C). The zygote develops a heavy wall with projecting spines, and passes into a stage of dormancy (Fig. 80, D).

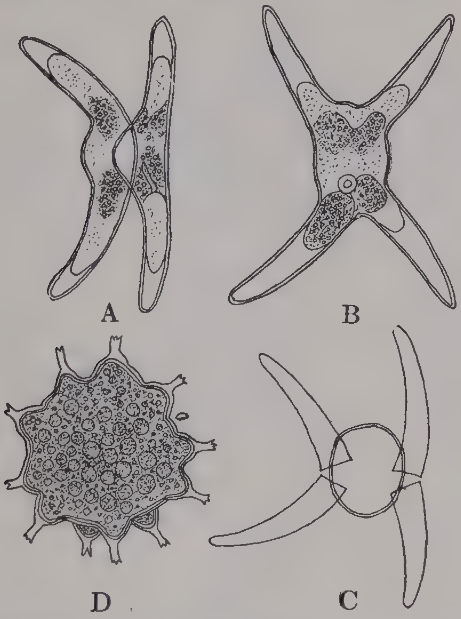

Fig. 80.—Formation of zygote in Desmids. A, two cells of Closterium coming together; B, the protoplasts fusing; C, the zygote formed. D, mature zygote of *Cosmarium botrytis* Menegh., showing spiny processes of the wall. (A, B, D, after DeBary; C, from "A Treatise on the British Freshwater Algae," by the late G. S. West; revised by F. E. Fritsch. Cambridge University Press, 1927.)

Germination of the Zygote.—According to Klebahn the gamete nuclei do not fuse until the beginning of the germination of the zygote (Fig. 81, A, B). As germination proceeds there occur two successive nuclear divisions, and the cell may also divide, so that each daughter cell will contain two nuclei, one of which will disorganize (Fig. 81, C, D, E). In this desmid, therefore, two individuals result directly from the zygote. The concluding steps in the process are shown in Fig. 81, E, F.

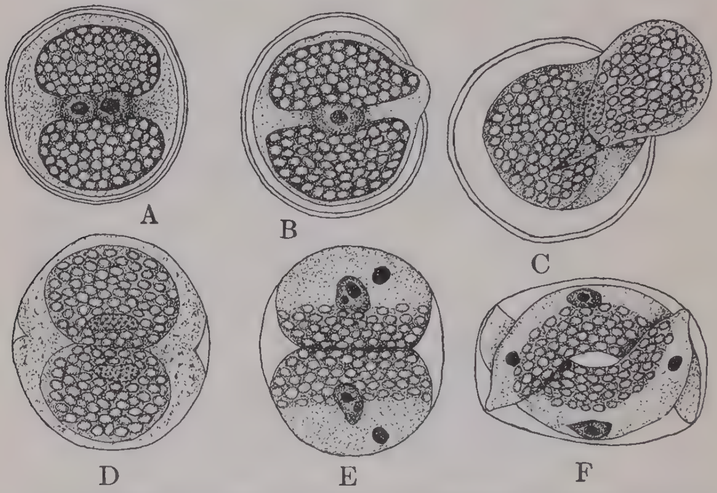

Fig. 81.—Fusion of nuclei of gametes and germination of zygote in Closterium. A, gametes with the two nuclei in contact; B, the nuclei have united and germination has begun; C, contents escaping from old wall of zygote; fusion nucleus in prophase of division; D, daughter nuclei formed; E, division of nuclei and cell division completed. In each daughter cell, one of the two nuclei is much smaller and denser; these small nuclei will disorganize. F, the daughter cells have begun to assume the form of the adult desmids; the degenerating nuclei lie in the ends of their respective cells. (After Klebahn.)

It is highly probable that the first mitosis following fusion in the zygote is a reducing division. The zygote, therefore, represents the diploid structure, while the individual desmid cells constitute the haploid structure.

DIATOMS—BACILLARIALES

Diatoms are unicellular plants varying greatly in form and size. All possess a characteristic structure due to the fact that the cell wall consists of two parts (valves), one fitting over the other like the two parts of a box. The cell wall is strongly impregnated with silica, which is

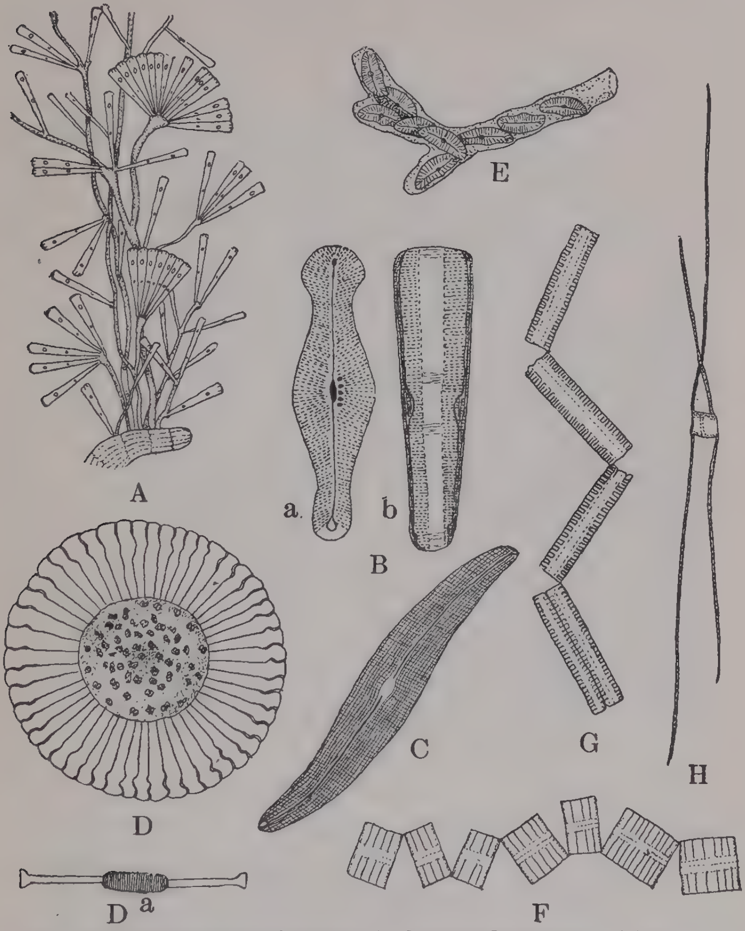

Fig. 82.—Some typical diatoms. A, *Licomorpha flabellata* (Carm.) Ag.: B, *Gomphonema geminata* (Lyngh.) Ag.; *a*, valve view; *b*, girdle view; C, *Pleurosigma attenuatum* (Kütz.) Wm. Sm.; D, *Planktoniella Sol* (Wallich.) Schütt.; *a*, valve view; E, *Cymbella caespitosa* Kütz.: F, *Tabellaria* flocculosa (Roth.) Kütz.; G. *Diatomum vulgare* DeBary; H, *Chaetoceras boreale* Bail. (From Engler and Prantl.)

variously marked by rows of minute pores. When all organic matter is removed from the cell, the remaining siliceous shell or skeleton presents the original shape of the diatom and reveals the characteristic markings. Because of these markings, many diatom shells are among the most beautiful objects of the microscopic world.

Diatoms are widely distributed over the surface of the earth, occurring on damp ground, on stones in moist places, and in both fresh and salt bodies of water, where they may constitute a very important element of the floating life known as *plankton*. They are sometimes so numerous as to impart a characteristic color to the water in which they are suspended.

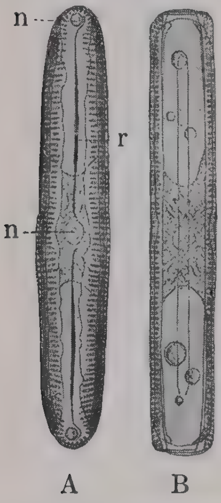

Fig. 83.—Two views of Pinnularia. A, valve view; B, girdle view. *n*, nodule; *r*, raphe. Note that one half-shell fits inside the other. (After Strasburger.)

Diatoms occur as isolated cells, or they may adhere, by means of a gelatinous substance, to form filaments or zigzag rows. In some species the cells are enclosed in gelatinous tubes; in others the cells develop gelatinous stalks, by which they are fastened to objects in the water, forming colonies (Fig. 82, A, E). The gelatinous substance is produced by the protoplast and exuded through pores in the cell wall.

Structure of the Cell.—As an illustration of cell structure we shall select some large form like Pinnularia or Navicula (Fig. 83, A, B). As stated, the cell wall consists of two halves, or *valves*, one fitting into the other like a box and its overlapping lid. In many diatoms the two halves are symmetrical, but in others they are not. Each valve consists of two parts, the top and the margin, or *girdle*. The top corresponds to the top or the bottom of the box, and the girdle to the overlapping sides of the box and its lid. The cell is described as seen from the valve view and from the girdle view.

In the valve view of Pinnularia (Fig. 83, A) markings are seen extending from the margin toward, but not reaching, the center. The central smooth place shows at its middle and at each end, strongly refractive spots, the *nodules* (Fig. 83, A, *n*). From each end nodule a line extends to the middle nodule. This line, the *raphe*, is a cleft or series of pores leading to the interior of the cell (Fig. 83, A, *r*). Through such openings as these the mucilage produced by the protoplast exudes.

The cytoplasm of the cell forms a wall layer with a bridge-like mass extending across the center, in which the nucleus lies. This bridge is best seen in the girdle view (Fig. 83, B).

Two chloroplasts are present in Pinnularia, in the form of large plates extending the length of the cell. In the girdle view (Fig. 83, B) they are seen from the flat side, while in the valve view their edges are turned toward the observer (Fig. 83, A). The chloroplast is of a golden brown or straw color. Its yellowish pigment is a mixture of chlorophyll and the yellow pigment *carotin*, or *xanthophyll.* The pigment of the plastid is sometimes referred to as *diatomin.* In some species, Cocconeis, for example, there is but one chloroplast. In many the chloroplast is very irregular in form.

Reserve food material is in the form of oil.

Vegetative Propagation, Cell Division.—When the cell is ready to divide, the protoplast increases in size, pushing the two valves apart until only the edges touch. Following the division of the nucleus and chloroplasts the cytoplasm divides, and the two cells lie within the old one, the two new valves lying back to back (Fig. (Fig. 84, A-D). In Fig. 85, C and D are cross sections of A and B respectively. Of the two diatoms thus formed, one is of the same size as the parent cell, but the other is smaller. After many such divisions, it is evident that a considerable reduction in the size of the individual will result.

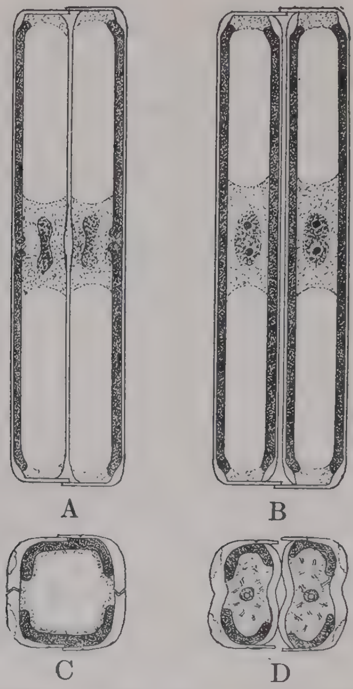

Fig. 84.—Cell division in Pinnularia. A, cell contents have enlarged and divided; the two half-shells have been pushed so far apart that the edges merely touch; the new half-shells have not yet been formed. C, a cross section of A. B, cell division is complete; each new half-shell fits inside the old one. D, cross section of B. (Figures adapted, A, B, after Lauterborn; C, D, after Engler and Prantl.)

Vegetative Propagation and Rejuvenescence.—The diminution in size just mentioned is counteracted by a process of rejuvenescence, which may or may not result in cell multiplication. One of the simplest cases is illustrated by *Melosira varians* Ag. (Fig. 85, A-C). Here the protoplast enlarges to two to four times the original size of the cell, forcing apart the valves. In this condition the cell has been called an *auxospore*, meaning "enlarging cell." This newly enlarged cell now develops a cell wall, and an enlarged diatom results. In some cases cell division accompanies auxospore formation, and there results cell multiplication as well as rejuvenescence.

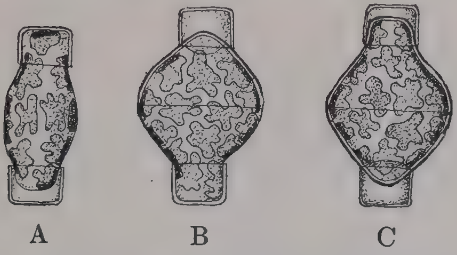

FIG. 85.—Auxospore formation in *Melosira varians* Ag. A, the halves of the shell have been pushed apart by the enlarging of the protoplast; B, C, the enlargement completed. These cells will develop new shells, and larger individuals will result. (Adapted from Engler and Prantl.)

Sexual Reproduction.—The formation of the zygote bears a close resemblance to that in the desmids. One of the simplest cases has been described by Karsten for *Cocconeis placentula* Ehr. The two cells come into contact, and the contents of each contract. The nucleus of each has divided in the meantime, resulting in one large and one small nucleus (Fig. 86, A, B). During contraction each cell surrounds itself with a gelatinous envelope. Near the point of contact of the two individuals the halves of the cell separate somewhat. From the opening in one of the cells, which is regarded as the male gamete, a small papilla protrudes, which grows toward the opening in the female cell, and the gelatinous envelopes are soon in open communication. The entire contents of the male cell now pass through this narrow channel and unite with the female cell (Fig. 86, C, D, E). The two large nuclei eventually fuse, while the two small ones disappear (Fig. 86, F). The zygote increases in size and a new cell wall is formed. In the meantime the two chloroplasts are reduced to one. What has happened in the case of the chloroplasts?

A more complex process is shown in *Rhopalodia gibbia* according to Kelbahn (Fig. 87, A-D). The two individuals place themselves side by side, being held together by the gelatinous secretion. The protoplast of each undergoes rejuvenescence, and two successive nuclear divisions take place. Each cell now divides by constriction, and two nuclei pass to each daughter cell, one nucleus remaining functional, and the other disorganizing. Each individual diatom has thus produced two

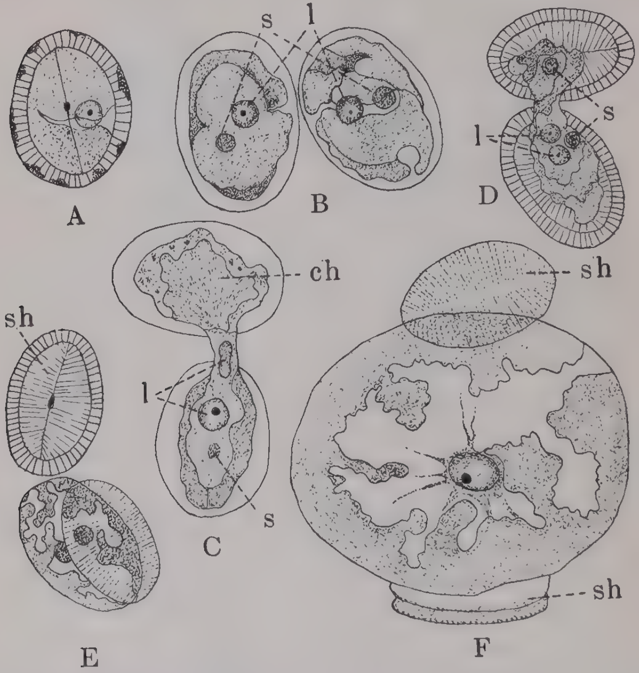

Fig. 86.—Formation of zygote in *Cocconeis placentula* Ehr. A, interior of cell, showing nucleus and one half of shell; B, two cells close together, the nucleus in each cell having divided, one of the daughter nuclei (1) being large, and the other (*s*) smaller; C, the protoplasts of the two cells have united; the large nucleus of the upper cell is in the narrow connection joining the two cells; D, the two large nuclei lie side by side; the small nuclei are degenerating the two halves of the shell lie in position; E, the contents of the two cells have fused; F, the zygote has increased in size. *ch*, chromatophore· *sh*, empty shell. All figures × 1000. (Redrawn from Karsten.)

gametes (Fig. 87, A). The gametes of one individual now meet, by means of protuberances, with those of the other, and fuse. The functional nuclei also fuse (Fig. 87, C, D). The two zygotes soon assume the definitive form of the parent cells, and develops a cell wall. The mucilaginous substance dissolves, and the new diatoms are set free.

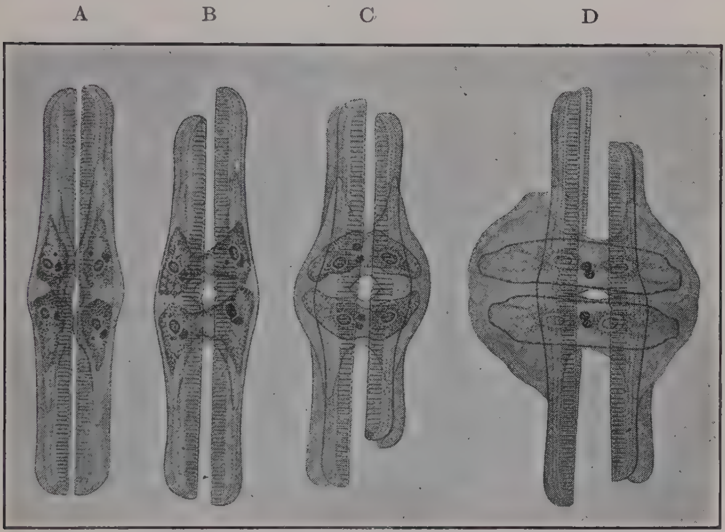

FIG. 87.—Formation of zygote in *Rhopalodia gibba.* A, conjugating pair seen from the valve side; protoplast of each has divided into two daughter cells, the gametes; each gamete contains, besides the large pyrenoid, a large and a small nucleus. B, cytoplasmic fusion of the two pairs of gametes has taken place; the small nuclei are scarcely recognizable. C, a later stage; the small nuclei have entirely disappeared, while the two functioning nuclei in each zygote, which has now changed from a dumb-bell to an elongated form, have come nearer together. D, the two young zygotes have elongated and begun to assume the adult form; gametic nuclei now in contact; cells surrounded by a gelatinous mass. (After Klebahn.)

It is clear from the foregoing that a zygote is very different from an auxospore, however much they may seem to resemble, and that the term *auxospore* should not be applied to the zygote.

In the two processes of sexual reproduction just described rejuvenescence takes place, but multiplication occurs only in the latter case. The author is of the opinion that the "auxospore" described in the foregoing does not represent a degenerate process of reproduction, but a means of rejuvenescence, coupled in some cases with vegetative multiplication.

If, during the nuclear divisions preceding the union of the gametes in Cocconeis and Rhopalodia, a reduction in the number of chromosomes takes place, the diatoms represent the diploid structure, and the gametes the haploid structure.

Role of Diatoms in Nature, and Their Use to Man.—Because of their great abundance at times, especially in the sea, and because of their direct importance as food for animals, and indirectly for man, diatoms have been styled "grasses of the sea." This fact may be illustrated as follows: Small crustaceans, such as Copepods, feed upon the diatoms. Larger animals, as herring, feed upon copepods, and still larger fishes feed upon herring, and some of these larger may be used as food by man. Their study as food for animals has been neglected until recently.

In past geologic ages the siliceous skeletons of diatoms formed extensive deposits known as "diatomaceous earth" or "kieselguhr." The extent of some such deposits give some idea of the great abundance of these plants existing at the time. While these deposits belong to comparatively recent geologic time, the plants may have existed at a much earlier period, but not in sufficient quantity to make their discovery certain. Diatomaceous earth has been used as an abrasive, as a base in the manufacture of dynamite, as a bacteriological filter, and in the manufacture of glass and porcelain. Because of their fine markings, the shells are used as test objects for microscope lenses. The beauty of the sculpturings of some shells entitles diatoms to the distinction of being spoken of as "jewels of the plant world."

Movement of Diatoms and Desmids.—Certain diatoms exhibit definite gliding movements, resembling the progressive movement of a tiny boat. The motion may proceed in one direction for a time, then in the opposite direction, or the direction may change at almost any angle. Only those diatoms that are in contact with some solid object move in this way. Those that live floating in the surface of the water do not exhibit such movements. No protoplasmic protrusion through the shell in the form of cilia or pseudopodia have been demonstrated.

Certain desmids, like Closterium, show slow movements, by which they apparently creep up the walls of an aquarium, and others that are orientation movements in response to light. Cytoplasmic protrusions through the wall of desmids have not been demonstrated, so that neither the diatoms, desmids, nor blue-green algae have any protoplasmic organs of locomotion.

According to Lauterborn, the gelatinous substance exuded through the pore or pores in the diatom shell swells up greatly in the water, and when resting against a support, the exuding mucilage pushes the cell forward away from the support. Diatoms floating in the surface of the sea are said not to have pores in the shell for the exudation of the mucilage, and these diatoms do not exhibit the gliding or crawling motion.

Desmids that live as isolated cells may exhibit a gliding and pendulum-like movement, both of which may be influenced by light and gravity. Those like Closterium, for example, build up the mucilage at one end, which on swelling lifts the cell. These crescent-shaped cells may be seen standing on one end, the other end being free, when they may swing about and be inclined toward the light. In this position they may bend over, becoming attached to the other free end, and the process is repeated. By a continuous series of such somersaults the cells move over the surface.

PROTOCOCCALES

The Protococcales include various forms, from unicellular, isolated individuals, such as Protococcus, to definitely organized colonies, as in Pediastrum and the water-net, Hydrodictyon. They occur chiefly in fresh water, ranging from a purely aquatic habitat to almost xerophytic conditions. Many that can live on moist surfaces are found on tree trunks, shaded earth, stones, etc. Certain forms constitute the algal constituent of many lichens, while others live in the intercellular spaces of aquatic seed plants, and still others impart the green color to such animals as fresh-water hydra and sponges.

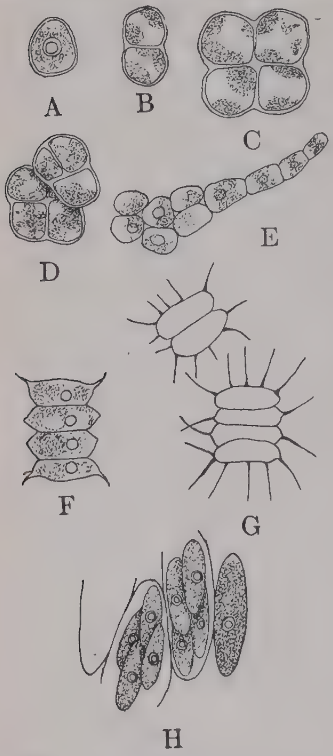

Fig. 88.—Protococcus and Scenedesmus. A-E, *Protococcus viridis* Ag. (*Pleurococcus vulgaris* Menegh.) A, a single cell; B-D, colonies of various sizes; E, the "protoderma" state. F, G, H, Scenedesmus; H, formation of new colonies from cells of an old colony. (A, C after Timberlake; B, D, E after Campbell; H, adapted from West.)

Protococcus (**Pleurococcus**).—As one of the simplest representatives we shall select Protococcus, usually found in abundance on the shaded side of tree trunks, buildings, and walls, and on moist ground. The cells are globular when isolated, or flattened on one or more sides when adhering in clusters or in loosely and indefinitely organized colonies (Fig. 88, A to D). Protococcus is never motile. Each cell has a firm wall, a nucleus, and, according to West, a parietal and much lobed chloroplast. Propagation is purely vegetative by the division of the cells (Fig. 88, B, C, D). As stated, the plant is adapted to a wide range of conditions of moisture and temperature. On tree trunks, for example, the cells may remain viable in the xerophytic condition through long periods of drought in either winter or summer.

Scenedesmus.—This plant generally occurs in colonies of a small number of somewhat elongated cells adhering side by side (Fig. 88, F, G). The end cells of the colony in some species may bear two or more short spines. Propagation is purely vegetative. In the simplest forms, each cell may divide lengthwise into two or more cells to form new colonies (Fig. 88, H).

Chlorococcum.—The spherical cells of Chlorococcum are found in water or in moist places. Some are said to constitute the algal portion of certain lichens. The plant propagates asexually by the production of one or more biciliate, motile cells, *swarm cells*, which excape from the parent cell, swim about for a time, and finally come to rest to form new individuals.

Chlorella Vulgaris Beijr.—This is a widespread alga, which sometimes lives symbiotically in the cells of *Hydra viridis* and in such Infusoria as Paramecium and Stentor.

Pediastrum.—This plant consists of a definitely organized colony of cells in the form of a flat plate; the number of cells in the colony is usually some power of two. As an illustration we shall use a common species, as shown in Fig. 89, A. Here we see that the colony consists of a flat, circular disc of sixteen cells. Each peripheral cell has two spines. In the young colony each cell has but one nucleus; but later the cells become multinucleate. Individualized chloroplasts are not recognized in the cells, the chlorophyll apparently being diffused in the outer layer of the cytoplasm.

Asexual Reproduction.—Asexual reproduction is accomplished by motile cells, any cell of the colony being capable of producing a new colony. The process is as follows: Nuclear division takes place in the cell until the number of nuclei equals the definite number of cells in the colony. By cleavage uninucleate cells are now formed (Fig. 89, A, *a* and *b*). The cell wall opens by a slit, and the biciliate swarm cells escape in a colorless envelope or vesicle, as in Fig. 89, A, *b* and B.

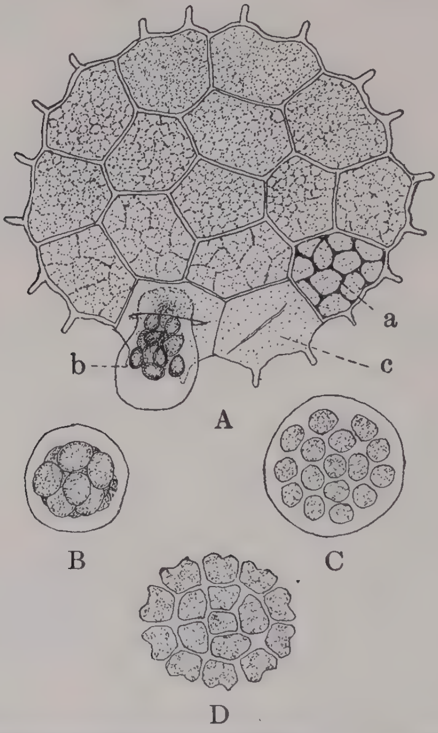

Fig. 89.—Asexual reproduction in Pediastrum. A, a 16-celled colony of *Pediastrum Boryanum* (Turp.) Menegh., cells of which are forming new colonies. *a*, cell forming swarm cells; *b*, escape of swarm cells in gelatinous envelope; *c*, empty cell from which swarm cells have escaped. B, vesicle containing swarm cells after their escape from parent plant. C, swarm cells arranging themselves to form a new colony. D, a young colony after the dissolution of the gelatinous envelope.

They move about for a short time within the vesicle, and finally come to rest, arranging themselves as in the parent colony. In the meantime the cilia disappear (Fig. 89, C, D). The envelope then dissolves, and the young colony soon matures into the adult form.

Sexual Reproduction.—Sexual reproduction is accomplished by motile isogametes. The gametes are developed as in the case of the asexual swarm cells, but they are smaller, and a larger number are produced in a parent cell. These gametes, which possess two cilia, escape through an opening in the cell wall into the water, where they unite in pairs to form zygotes. The steps leading to the formation of new colonies from the zygote are similar to those in Hydrodictyon, which are described in the following paragraphs.

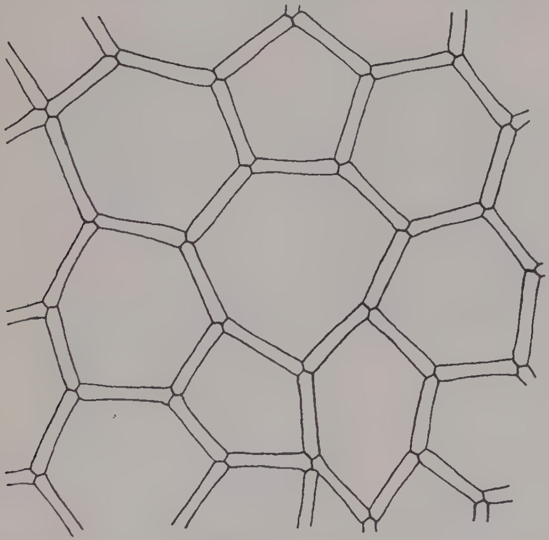

Fig. 90.—Portion of a colony of Hydrodictyon, showing the manner in which the cylindrical cells are attached to form a net.

Hydrodictyon.—The water-net is a definitely organized colony of many thousands of cylindrical cells united by their ends to form, as a rule, from three to six-angled meshes of a net (Fig. 90), the colony being in the form of a cylindrical or sleeve-like sac closed at both ends. These may attain a length of 20 or 30 centimeters, the cells frequently measuring a centimeter in length. In almost all nets some irregularities occur, some of the meshes having more than six sides, and others being open, leaving cells with unattached ends. In each cell, which has a firm cell wall, the multinucleate cytoplasm is distributed in a thin layer along the wall, the remaining

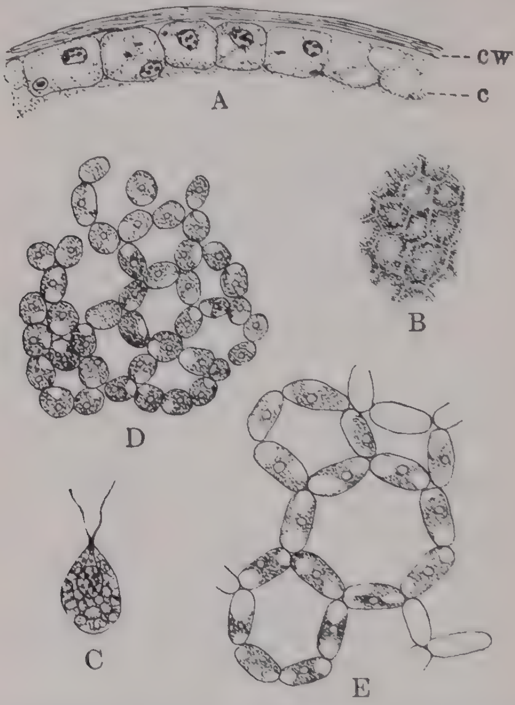

FIG. 91.—Asexual reproduction in *Hydrodictyon utriculatum* (L.) Lagerh. A, portion of wall layer of nucleated cytoplasm of a cell, showing cell cleavage; *cw*, cell wall; *c*, cytoplasm. B, Surface view of a few protoplasts that will become swarm cells. C, a mature swarm cell stained to show nucleus and starch grains. D, swarm cells coming together to form a net. E, a later stage than D, showing three meshes of a young net. (A and C after Timberlake; B, D, E, after Campbell. All greatly enlarged.)

cavity of the cell being occupied by the large vacuole. In the cytoplasmic layer the chlorophyll is somewhat uniformly distributed, there being no individualized chloroplasts. Numerous pyrenoids are present in the chlorophyll-bearing layer.

Asexual Reproduction.—Any cell of the net may give rise to a new colony. By a process of cleavage the protoplasmic contents of the cell will divide into thousands (estimated at 7,000 to 20,000) of naked swarm cells, each having one nucleus and two cilia (Fig. 91, A, B, C). These motile cells move about actively in the cavity of the parent cell for a short time, after which they come to rest and begin to form a new net (Fig. 91, D, E). The cells lose their cilia, elongate, and become attached by their ends in such a manner as to form the net (Fig. 92). The wall of the parent cell is now dissolved, and the young colony set free. The cells of the young net have but one nucleus, but, with further growth and repeated nuclear divisions, the cells of the adult net become multinucleate.

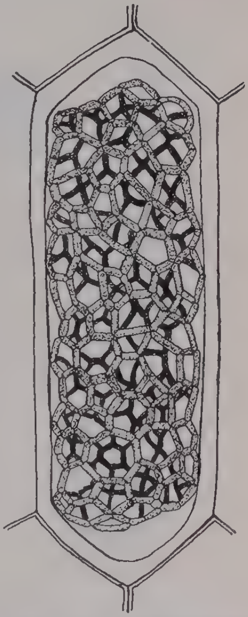

FIG. 92.—*Hydrodictyon utriculatum* (L.) Lagerh. A young net formed from swarm cells in a parent cell of an old net. (Adapted from Klebs.)

Sexual Reproduction.—In the same manner as in asexual reproduction the protoplasmic contents of any cell may give rise to very many (30,000 to 100,000) biciliate swarm cells that are smaller than those formed in asexual reproduction. These are the gametes. They escape from the parent cell, move about freely in the water, and unite in pairs to form zygotes (Fig. 93, A, B, C). Gametes from the same cell or from different cells may unite to form zygotes, and, because of this fact, Hydrodictyon is said to be monoecious.*

The zygotes move about for a time, then come to rest, and develop a firm cell wall (Fig. 93, C, D). According to Pringsheim, the zygotes will remain uninjured in the dry state if not exposed to the light. When they are kept in water, exposure to light does not impair their

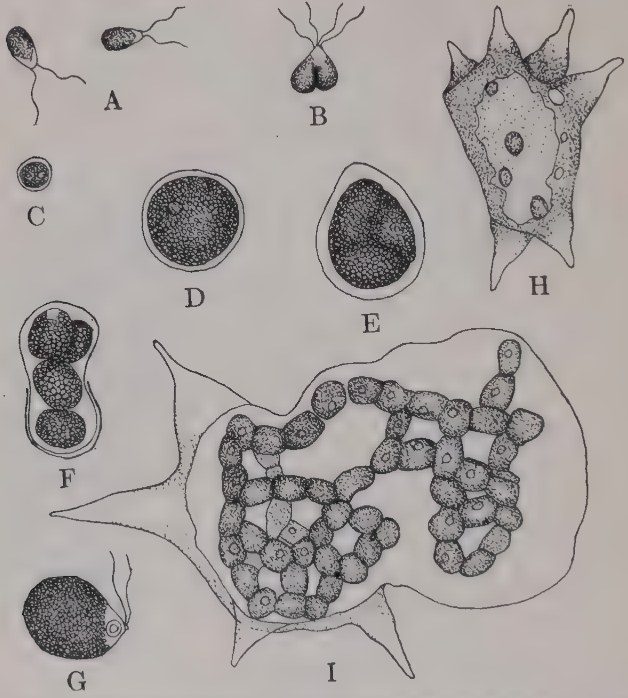

FIG. 93.—Sexual reproduction in *Hydrodictyon utriculatum* (L.) Lagerh. A, gametes; B, gametes uniting; C, zygote; D, zygote beginning to germinate; E, three of the four cells into which the contents of the zygote has divided; F, zygote in a later stage of germination; G, one swarm spore from a germinated zygote; H, mature polyhedron; I, formation of a small net from a polyhedron. (B, from Klebs; other figures from Pringsheim.)

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* A plant that produces gametes of both sexes is *monoecious;* it is a bisexual individual. When a plant produces gametes of but one sex, the individual is *dioecious,* two different individuals being necessary for the production of the gametes. Such individuals are unisexual.

ability to germinate. Prior to germination the zygote undergoes a period of growth, by which it increases greatly in size and takes on a deep green color (Fig. 93, D). The contents then divide to form two to five biciliate swarm spores that escape through a rupture in the outer wall in a gelatinous vesicle (Fig. 93, E, F, G). This vesicle dissolves, and the swarm spores are set free. After swimming about for a time, each comes to rest and develops into a large cell having several conical or horn-like protuberances (Fig. 93, H). These cells have been named "polyhedra," because of their resemblance to a plant described under the name *Polyedrium.*

The contents of each polyhedron gives rise to swarm cells. The inner layer of the cell wall becomes mucilaginous, and by swelling ruptures the outer cuticle-like layer and escapes as a gelatinous vesicle, in which the swarm cells move about. They finally come to rest and form a new net, which is set free by the dissolution of the vesicle (Fig. 93, I). The nets arising from the polyhedra are relatively small, being composed of 200 to 300 cells, whereas the number of cells of a colony developed from a cell of an adult vegetative colony has been estimated by Alexander Brown to be as high as 30,000.

VOLVOCALES—ROLLING ALGAE

The Volvocales, like the Protococcales, occur in the form of unicellular individuals and colonies. They differ from the latter in being always motile in the active vegetative condition. The organization of the colony varies from that of simple, undifferentiated forms, as in Gonium, to those that are highly differentiated, as in Volvox.

Pandorina.—As an illustration of the complete life cycle in a simpler colony, Pandorina, which is commonly found among other fresh water algae, and easily recognized, may be selected. This plant consists of a globular colony of sixteen cells surrounded by a firm gelatinous envelope. Each cell is broadly ovoid or conical, or frequently angular by pressure of contact, with the narrow end next to the center. From near the center of the broad outer side of each cell spring two cilia which extend through the gelatinous membrane into the water. Near the base of the cilia is a red pigment- or eye-spot. The chloroplast contains a pyrenoid. The colony is undifferentiated, the cells being alike in every respect (Fig. 94, A).

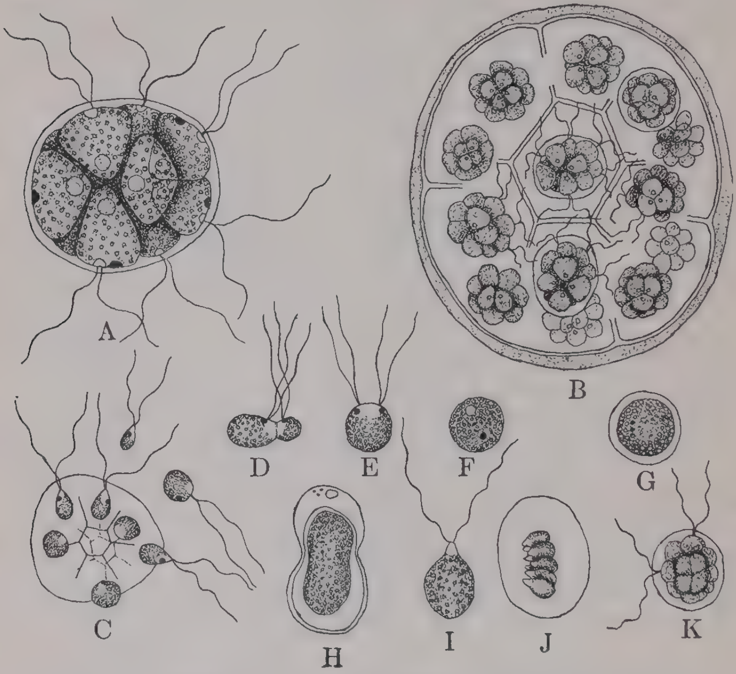

Fig. 94.—Life history of *Pandorina morum*. A, a mature colony of 16 cells; B, sixteen young colonies resulting from asexual reproduction, all held in the gelatinous envelope of the parent colony; C, gametes escaping from the gelatinous mass of the parent colony; D, E, F, union of gametes in pairs; F, young zygote; G, mature zygote, just prior to germination; H, germinating zygote; I, one of the swarm spores resulting from the germination of the zygote; J, K, young colonies produced by the division of single swarm spores. All figures × 850. (After Pringsheim.)

Asexual Reproduction.—In asexual reproduction each cell, by four successive divisions, gives rise to a new colony. Each cell of the new colony develops two cilia and the pigmented spot. A gelatinous envelope is formed about each colony, and the new colonies are set free by the disintegration of the original gelatinous envelope (Fig. 94, B).

Sexual Reproduction.—Cells of the colony may also give rise to a large number of small, biciliate gametes, which escape from the envelope and move about freely in the water (Fig. 94, C). If the cells are of the same size they are termed *isogametes*, there being no distinction in sex. But, if, as may also happen, the gametes are of unequal size, the larger are regarded as the female and the smaller as the male gametes. When the two gametes are unequal in size they are referred to as *heterogametes*.

The gametes unite in pairs to form zygotes, which continue to move about for a time but finally come to rest, developing a firm cell wall, and assuming a bright red color (Fig. 94, D, E, F, G). After a period of rest and the return of suitable conditions for growth, the zygotes will germinate, giving rise to two or four swarm spores (Fig. 94, F, I). Each swarm spore may now divide, giving rise to a new colony of sixteen cells (Fig. 94, J, K). It is reasonable to suppose that the zygote represents the diploid structure of Pandorina.

Chlamydomonas.—Chlamydomonas is a rather common unicellular form. The cell bears two cilia and has a large, cup-shaped chloroplast in the thick bottom of which is a pyrenoid. Near the anterior end of the cell are contractile vacuoles and a red pigment spot (Fig. 95). Chlamydomonas reproduces both sexually and asexually after the manner of Pandorina. *Chlamydomonas nivalis* (Bauer) Wille. is usually blood red in color, owing to a pigment, haematochrome. The thick-walled, non-motile forms sometimes occur in large quantities on snow in high altitudes, when they are known as "red snow."

Haematococcus pluvialis Flotow (*Sphaerella lacustris* Hazen), also deep red in color, is commonly found in shallow pools, where the resting cells form a dull red coating on the bottom or on any contained objects when the pool dries up. This fact has given rise to the expression "red rain." Haematococcus differs from Chlamydomonas in having protoplasmic threads that pass out into the cell wall.

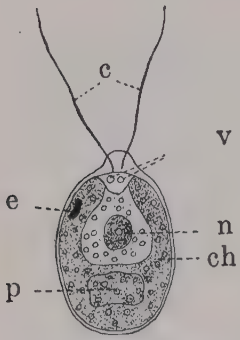

Fig. 95. — *Chlamydomonas angulosa* Dill. *c*, cilia; *e*, eye spot; *ch*, chloroplast; *n*, nucleus; *p*, pyrenoid; *v*, vacuoles. (After Dill, according to Oltmanns.)

Volvox.—The most highly differentiated forms of the Volvocales are found in the genus Volvox. *Volvox globator* the species most commonly encountered, consists of thousands of very small, pale green, pear-shaped cells embedded near the surface in a hollow sphere of gelatinous substance. Each cell has a chloroplast, a nucleus, an eye-spot, and two cilia attached at the anterior end (Fig. 96, A, B). The cells are connected with one another by cytoplasmic threads. The colonies are often more than half a millimeter in diameter, and may readily be seen with a hand lens as pale green spheres rolling through the water. Because of the cytoplasmic connections between the cells, and the highly differentiated gametes, it is questionable whether Volvox should be regarded as a colony (coenobium) or as a definite multicellular individual. Volvox is not in the form of an exact sphere, but one which is very slightly oval. The smaller end contains few or no vegetative reproductive cells. This smaller end of the oval may be regarded as the anterior end of the plant and the opposite side the posterior end.

Asexual Reproduction.—Certain vegetative cells will increase greatly in size and move into the hollow of the sphere. Here, by successive divisions, a small, rounded, flat disc is formed, then a bowl, and finally a closed sphere. Three or more colonies may thus be developed within the central cavity of one parent colony (Fig. 96, A).

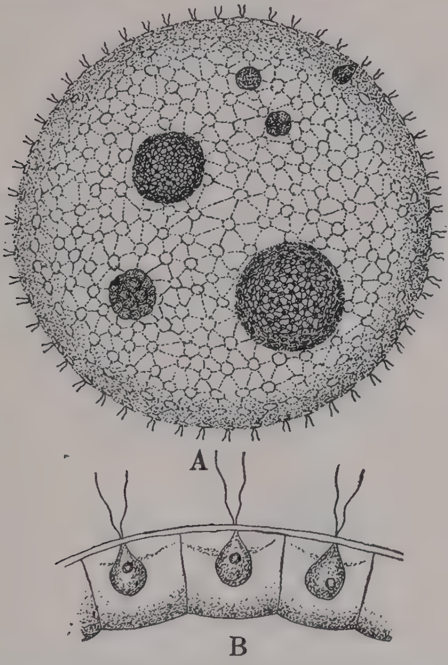

FIG. 96.—Volvox. Structure and asexual reproduction. A, adult colony containing two young colonies, and four stages in the development of the colony from vegetative cells. B, portion of the gelatinous periphery of the colony, showing position of the vegetative cells.

The parent colony, rolling gently through the water, with two or three smaller colonies rolling within it, is a fascinating sight when seen with the microscope.

Sexual Reproduction.—Volvox has two kinds of gametes: small motile sperms and large, non-motile eggs. The sperm is a pale yellowish, club-shaped cell with a slender, tapering anterior end. It has two cilia inserted laterally, and an eye spot (Fig. 97, B). A large number of sperms are formed from a single vegetative cell which enlarges and passes into the interior of the colony, where it undergoes repeated divisions in one direction (Fig. 97, A, *s*). Certain other vegetative cells, which have enlarged and passed into the central cavity, become eggs (Fig. 97, A, *e*). There they unite with sperms to form zygotes. The zygotes assume a reddish color and develop a thick wall, the outer layer of which becomes spiny (Fig. 97, C). After a period of dormancy the zygote germinates, giving rise to a new colony.

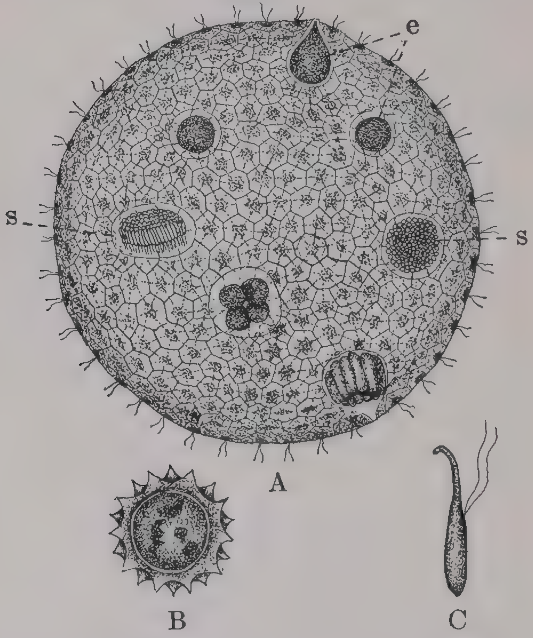

Fig. 97.—Sexual reproduction in Volvox. A, monoecious colony bearing eggs (*e*) and sperms (*s*). C, one sperm, showing shape, eye-spot, and cilia. B, mature zygote provided with a thick, spiny wall. (Redrawn from chart by Leuchart.)

Response to Light.—Motile plant cells, especially among the algae, whether representing the vegetative or reproductive condition, are usually influenced in the direction of their movements by chemical substances and by forces of the environment which affect them as stimuli. The cells are said to *respond* to the given stimulus. For example, if Pandorina, or any other of the Volvocales, be held in a glass vessel so that the light enters from one side, as near a window or an artificial light, the plants will soon collect along the wall of the vessel next to the window or next to the source of light. If observed in a hanging drop under the microscope, they will be seen to move toward the edge of the drop next to the source of illumination. The light does not cause the plants to move, it merely influences the *direction* of their locomotion. If the light be too dim, there will be little or no response, and if it be too intense, the plants may move in the opposite direction, that is, away from the source of illumination. The response that motile plants make to light in this manner is termed *phototaxis*. Movements toward the source of illumination, or toward any source of stimulus, represent a *positive* response (as positive phototaxis); movement directed away from the source of the stimulus is a *negative* response (as negative phototaxis).

It should be remembered that an organism will respond normally to stimuli only when the intensity of the energy falls within a certain range. The extremes represent intensities beyond which no response is perceptible. The lower limit is the *minimum*, the upper, the *maximum*, and that intensity or degree of energy which calls forth the best response is the *optimum*. Strong electric light concentrated upon the plants may kill them instantly.

Generally speaking, motile plant cells provided with eye-spots are more sensitive to light than those in which such a body is absent. This fact has led to the view that the eye-spot represents a part of the cytoplasm which is especially sensitive to light. Do you think the response to light is of any advantage to the plants in question in their adaptation to the environment? Or has the response to light any "survival value"?

CONFERVOIDEAE

The confervoid algae include the majority of the common filamentous forms, which are very widely distributed in both fresh and salt water. They represent a wide range of variability both in vegetative structure and in methods of reproduction. In vegetative structure they range from very simple unbranched filaments to a more massive and leaf-like thallus, as is illustrated in Ulva, or sea lettuce. As concrete cases for detailed presentation we shall select Cladophora and Oedogonium, the former representing a simple method of sexual reproduction in which both gametes and gametangia are undifferentiated, while in the latter the sexual cells are highly specialized. Other forms commonly found in ponds and streams will be described very briefly.

Cladophora.—Cladophora consists of branched filaments differentiated into base and apex. The filaments are usually attached to some object in the water by means of the basal cells, which are modified into organs of attachment, or holdfasts. Some forms branch very profusely and form relatively short, dense, bushy tufts (Fig. 98, A). During the spring and early summer months the growth of some forms is so prolific that the immense, ropy masses almost clog the small streams in which the plant is common.

The branches always arise from the upper (distal) ends of the cells (Fig. 98, B). Growth in length of the filaments is confined chiefly to the terminal portions, though cell divisions not infrequently occur in the older parts of the plant. For details of cell division see page 10.

Structure of the Cell.—The cells have a firm and rather thick, stratified wall, to which may often be attached diatoms and other small algae, together with particles of other foreign matter, all of which help to impart a noticeable harshness to the mass. Numerous nuclei, pyrenoids, and chloroplasts are present in the

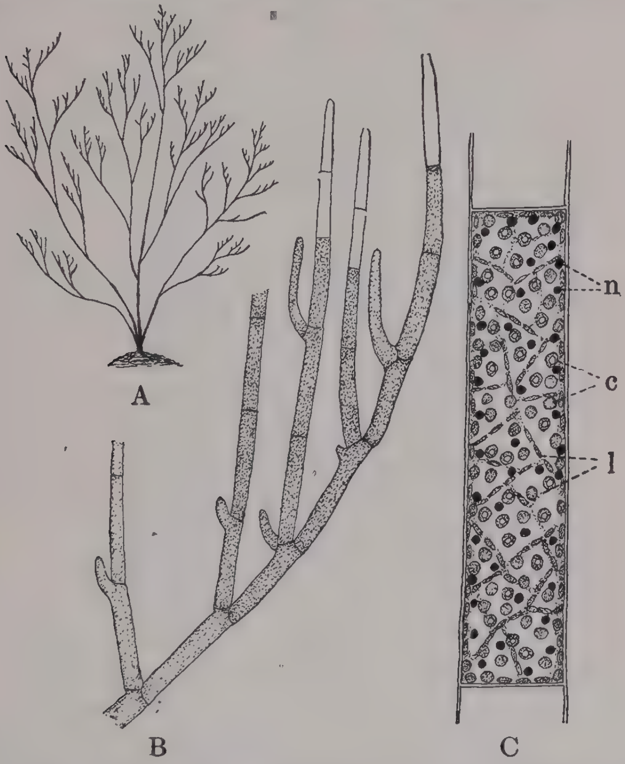

Fig. 98.—Cladophore (Sp.) A, sketch of a tuft of plants attached to a rock or other substratum. B, small portion of a plant, enlarged, showing method of branching; swarm spores or gametes have escaped from the empty cells at or near the tips of some of the branches. C, an actively growing vegetative cell, enlarged, showing the numerous nuclei, *n*, chloroplasts, *c*, and cytoplasmic lamellae, *l*; the chloroplasts distributed along the latter are seen from their edges.

larger adult cells. The chloroplasts are rounded, but in older, well nourished cells they may become polygonal because of crowding. The central part of the cell is occupied by a large vacuole, which, however, is traversed by flat cytoplasmic plates, or lamellae, which meet and intersect in such manner as to divide the vacuole into cell-like compartments. The chloroplasts are confined principally to the wall-layer of cytoplasm, although a few may be located upon the lamellae (Fig. 98, C).

Asexual Reproduction.—Cladophora reproduces asexually by means of swarm spores. These are commonly developed in the cells of the younger branches. In the formation of swarm spores the contents of the cell, by cleavage, give rise to a number of naked cells, which escape through a small opening in the upper end. The cell that produces spores is called a sporangium (Fig. 99, A). The swarm spores have four cilia, which arise near the base of a small beak at the anterior end, an eye-spot, one nucleus, and two or more chloroplasts (Fig. 99, B). In some species asexual swarm spores with but two cilia have been reported. After moving about for a time the spore comes to rest and develops into a new filament. On coming to rest the swarm spore usually attaches itself to some object, the beak at the anterior end developing into the holdfast.

Sexual Reproduction.—Sexual reproduction is accomplished by motile isogametes, each provided with two cilia. They are much smaller than the asexual swarm spores. As in the case of asexual reproduction, the cells of the smaller branches may, without undergoing any external change, become gametangia (Fig. 99, C). Here the contents of the cell give rise to a larger number of cells which escape as gametes. Each has two cilia, a red eye-spot, a nucleus, and one or more chloroplasts (Fig. 99, D). They unite in pairs to form zygotes (Fig. 99, E, F, G). The zygote is said to germinate immediately (Fig. 99, H). The gametes may start to develop into new plants without uniting, but the resulting plantlets are small and feeble.

The fresh water forms of Cladophora do not produce swarm spores or gametes readily, but in certain marine species, if the plants be brought from the sea and placed in shallow dishes, the swarm spores and gametes will be developed in large numbers over night. Both swarm spores and gametes are sensitive to light and lend themselves readily to experimentation.

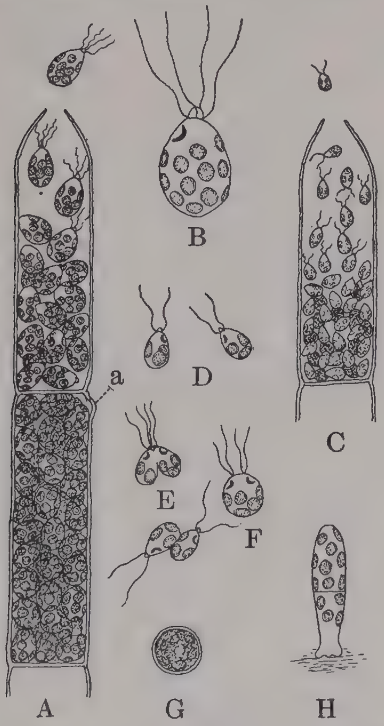

FIG. 99.—Cladophora. Asexual and sexual reproduction. A, two cells at the end of a branch, which have become sporangia. Swarm spores escaping from the terminal cell; those in the cell below almost mature; *a*, place at which the opening of the sporangium will be formed. B, a single swarm spore, greatly enlarged, showing the four cilia, the eye-spot, and the chloroplasts. C, a gametangium, from which gametes are escaping. D, gametes greatly enlarged, showing the two cilia, the eye-spot, and the chloroplasts. E, gametes uniting in pairs. F, a young zygote, in which the characteristics of the gametes are still seen. G, mature zygote. H, a young plant resulting from the germination of a swarm spore would be similar to this in appearance. (Figures somewhat diagrammatic; from a species collected in the Bay of Naples.)

Some species of Cladophora are annual, while others seem to live from year to year. In the latter, the larger portion of the plant dies, but the basal portions persist, the cells becoming filled with food material. These cells give rise later to new filaments vegetatively; or it is probable that they may develop swarm spores.

Aplanaspores.—Many of the Confervoideae develop what are known as *aplanaspores*, which serve to propagate the plant. In the production of these the contents of the cell contract and form a new cell wall within the parent cell. These aplanaspores lie dormant during periods unfavorable for vegetative activity but germinate on the return of favorable conditions, growing into new plants. If vegetative cells merely thicken the wall of the old cell without forming a new wall as described for aplanaspores, and give rise to new plants in like manner, such cells are called *akinetes*.

Ulothrix.—Ulothrix consists of delicate, unbranched filaments, whose rather short, uninucleate cells are all alike except the basal or holdfast cell. The chloroplast is band-shaped with one or more pyrenoids. It frequently occurs in aquaria and in tanks or troughs used for watering stock.

Conferva.—Members of this genus consist also of unbranched filaments, in which the uninucleate cells have two to several disk-shaped chloroplasts, but no pyrenoids. Reserve food, if present, is in the form of oil rather than starch. The plant is found in ponds and streams along with other algae.

Chaetophora.—The copiously branched filaments of this alga are embedded in a rather firm gelatinous mass. The plant may be recognized as green, rounded masses of jelly, varying in size from two to ten millimeters in diameter, attached to stems and leaves or other objects in clear, running water in the spring. The branches of the filaments end in long, slender, colorless cells. The single chloroplast in the cell consists of a parietal band with one or more pyrenoids.

Stigeoclonium.—Stigeoclonium consists of branched filaments, but with little distinction between the branches and main filaments. The filaments are surrounded by a gelatinous substance, but not united into a compact mass as in Chaetophora. They end in slender, colorless cells.

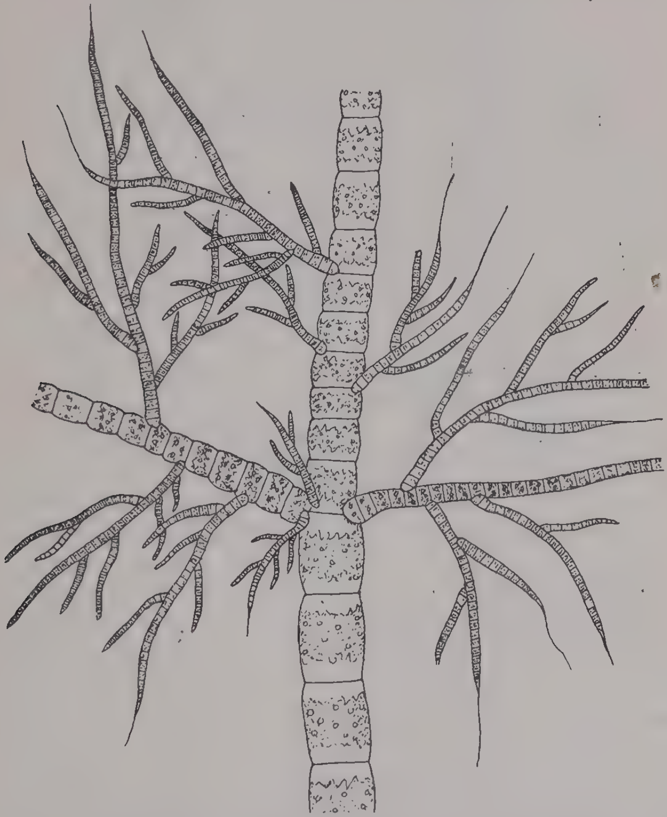

Fig. 100.—Draparnaldia. Portion of a plant showing structural habit.

Draparnaldia.—Draparnaldia is generally abundant in running water in early spring. It consists of a definite main filament or axis with tufted side branches of more limited growth. The main axis bears secondary axes which repeat the characteristic structure of the main axis. The whole plant is coated over with the gelatinous substance, and the branches may end in slender, colorless cells. In the cells of the main axis the chloroplast is in the form of a cylindric or parietal band, which may be perforated. Pyrenoids are present (Fig. 100).

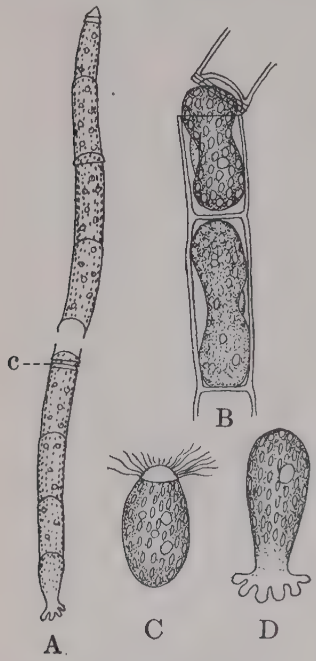

FIG. 101.—Oedogonium. A, the upper and lower ends of a vegetative filament; *c*, the cap-like markings at the upper end of certain cells. B, two cells, illustrating the formation of swarm spores, one spore being formed in each cell. C, a swarm spore, showing anterior colorless spot and the circle of cilia at its base. D, germination of a swarm spore. The colorless anterior end is sensitive to contact and develops into the holdfast.

Ulva.—The sea lettuce has the form of a large, leaf-like cell surface, two layers of cells in thickness. All species are marine.

Enteromorpha.—The plants of this genus are ribbon-shaped, either cylindrical or flattened. When young the plant body is two cells in thickness, but later it becomes hollow, the wall consisting of one layer of cells.

Oedogonium.—Oedogonium consists of usually deep green, unbranched filaments, strictly differentiated into base and apex, and ordinarily attached to some submerged object such as the stems and leaves of other plants. Adult plants may sometimes break away and float in masses. The basal cell of the filament, frequently in the shape of an Indian club, serves as the holdfast. The terminal cell may be rounded or pointed or elongated into a slender hair-like structure. Neither the basal nor the terminal cell ever undergoes division. The end of the basal cell which is attached is either flattened into a disk or developed into a number of short, finger-like branches (Fig. 101, A).

The cell wall consists of a relatively thick cellulose layer with a thin cuticle on the outside. Across the upper ends of certain cells may be seen two to several fine parallel lines by which Oedogonium may readily be distinguished from other unbranched filamentous algae similar to it in appearance (Fig. 101, A, *c*). These lines represent the edges of the so-called "caps."

The cytoplasm is chiefly disposed as a thin parietal layer in which the chloroplast is imbedded. The chloroplast is variable, but always parietal, and usually in the form of a net or reticulum. In the larger species the pieces of the reticulum may become separate and distinct. One or more pyrenoids may be present. The nucleus of the cell is usually centrally placed.

Cell Division.—Any cell of the filament, except the basal cell and the tip cell, is capable of division; but only certain cells undergo several successive divisions. These are the ones with the transverse lines or "caps" to which reference was made above. The caps indicate the number of times the cell has divided (Fig. 101, A, *c*). When a cell divides, one of the resulting cells possesses the old cell wall; the other has an entirely new cell wall except for the cap at the upper end. The new wall is formed during division as follows: In the upper end of the dividing cell a thick solid cellulose ring is formed next to the lateral wall (Fig. 102, A). After the nucleus has divided, or as it divides, a circular cut or split occurs in the cell wall along the line of contact between the wall and the cellulose ring (Fig. 102, B). The ring now stretches into a cylinder, which, with the cap at the top, becomes the wall of the upper of the two cells. The transverse wall of the dividing cell is formed just below the circular cut, so that the lower of the two cells has the old wall of the parent cell, while the wall of the upper is new, as stated above (Fig. 102, C, D). The transverse wall is formed by the fibers connecting the daughter nuclei, and not as in Spirogyra. The tip of the terminal cell of the filament is usually a cap.

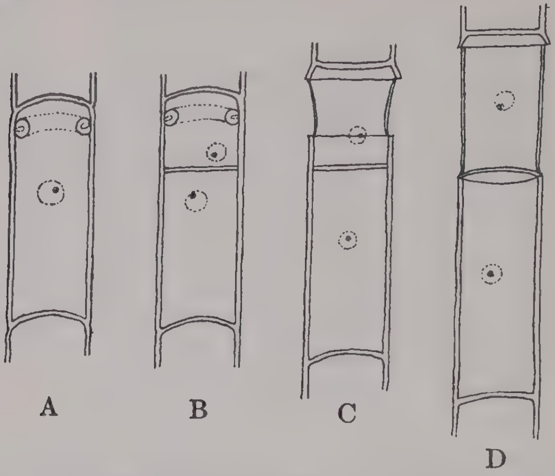

Fig. 102.—Cell division in Oedogonium. A, cell with thick ring of cell wall substance formed inside at the upper end. B, small cell and large cell formed by division of A. C, a circular split has occurred in the old cell wall entirely around the cell just opposite the middle of the ring; the ring has stretched in length to make a new wall for the upper cell. The part of the old wall above the circular split now forms a cap. D, the upper cell has elongated, and its lower end has moved upward to the top of the old cell wall. There have thus been formed two cells, the upper with an entirely new lateral wall and the lower completely enclosed in the old wall of the parent cell.

Asexual Reproduction.—Asexual reproduction is accomplished by large swarm spores, one being formed in a cell. Any cell of a filament, except a tip cell, may form a swarm spore. During the transformation of the cell contents into the swarm spore the cytoplasm contracts away from the cell wall by means of self-plasmolysis, and a lens-shaped, colorless area is seen at one side (Fig. 101, B). This colorless spot represents the anterior end of the mature swarm spore, and from the base of this spot a circle of many cilia will arise. The cell wall splits transversely near the upper end and the swarm spore escapes. It is generally oval in shape, with the colorless beak at the anterior end; from the base of the beak spring the cilia (Fig. 101, C).

The swarm spore does not have an eye-spot. After a short period of movement the spore comes to rest and germinates. The anterior colorless end becomes the holdfast of the new plant (Fig. 101, D). It will be seen that the longitudinal axis of the spore and of the new plant represents the transverse axis of the parent cell.

Sexual Reproduction.—The type of sexual reproduction seen in Oedogonium is one of the highest found in any of the green algae, both the gametes and the gametangia being differentiated sexually. The gametangium bearing the egg, or female gamete, is the *oögonoium;* that producing the sperms, or male gametes, is the *antheridium.*

Both monoecious and dioecious species are found in the genus. A dioecious species is selected for presentation here.

In this the female plants possess the normal size of the adult filament, but the functional male plant, known as the "dwarf male plant," is very small, consisting of only two or three cells. The dwarf male plants are usually, though not always, attached to the female plants just below the oögonium (Fig. 103, A, *dm*). The oögonium is rounded or barrel-shaped, and larger than the ordinary vegetative cells. It is usually formed from a cell that has divided many times, as shown by the numerous cap-like markings at the upper end (Fig. 103, A). The contents round off, and the chloroplast withdraws slightly from the upper end, forming the colorless "receptive spot." An opening in the cell wall is formed at one side near the upper end of the oögonium, and the egg is ready for fecundation.

The "dwarf male" in this species ordinarily consists of a basal cell and an antheridium. The antheridium bears two sperms (Fig. 103, A, *an*). The sperm is a very small, colorless, oval cell, with a circle of cilia at its anterior end. When the antheridium opens, the sperms escape, and one of them enters the oögonium and penetrates the egg, its cytoplasm mingling with that of the egg, and its nucleus fusing with the egg nucleus.

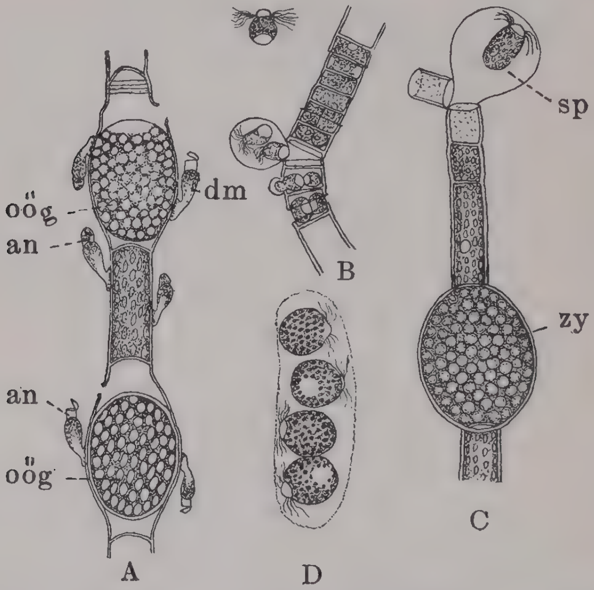

Fig. 103.—Oedogonium. Sex organs and germination of zygote. A, portion of filament with two oögonia (*oög*), and attached dwarf males (*dm*), bearing antheridia (*an*). B, portion of a filament that has given rise to antheridia, each containing two sperms. C, portion of a filament showing a mature zygote in an old oögonium, and an androspore (*sp*) developing from another cell. D, four swarm spores resulting from the germination of a zygote. (B, C, D, after Pringsheim.)

When fecundation is completed, the zygote develops a firm cell wall and passes into a period of dormancy. The mature zygote is reddish-brown in color, and various external markings are developed in some species. The reserve food is a fatty oil dissolved in a reddish-brown pigment (Fig. 103, C, *zy*).

Formation of the Dwarf Male.—The dwarf male plants which produce the sperms are developed from swarm spores formed by a plant similar to the oögonial plant. Certain cells divide transversely into a small number of short cells (androsporangia) each of which produces a small swarm spore, known as an *androspore*. Androspores are similar to the asexual swarm spores described in a preceding paragraph, though much smaller (Fig. 103, C, *sp*). They escape, move about in the water, and finally become attached and develop into the dwarf male plants. When androspores become attached to the oögonium, or to a cell near it the dwarf males are likely to be found as shown in Fig. 103, A.

Monoecious Species.—In monoecious species of Oedogonium antheridia are borne by the filament that produces oögonia. In such cases certain cells of the filament undergo transverse divisions into several short cells. Each of these is an antheridium and bears two sperms (Fig. 103, B). The sperms are smaller than the androspores.

Germination of the Zygote.—The zygote is set free by the decay of the wall of the oögonium. During germination the contents become green again and undergo divisions resulting in the formation of four swarm spores, which escape in a delicate vesicle when the cell wall is ruptured (Fig. 103, D). The vesicle dissolves, and the four swarm spores move about for a short time, finally coming to rest and developing into new plants. The zygote is doubtless the diploid structure, while the whole plant is the haploid structure.

Coleochaete.—Coleochaete is of special interest because its life history is suggestive of one way by which plants like the liverworts may have been developed from an alga-like ancestor.

The plant occurs in fresh water, commonly attached to the leaves and stems of aquatic plants. It consists of a flat, rounded or lobed disc of cells arranged in radial rows, or of radiating, branched filaments attached in part side by side (Fig. 104, A, C). In some species certain cells bear long, slender spines. The uninucleate cells contain each a parietal chloroplast with one or two pyrenoids.

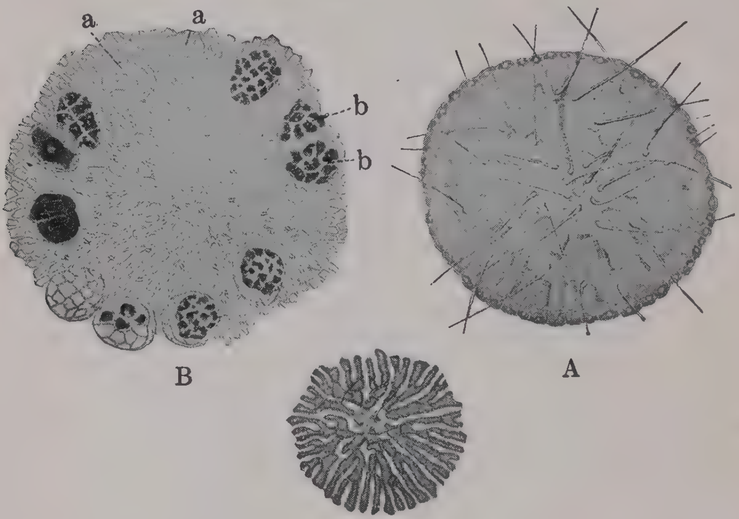

FIG. 104.—A, *Coleochaete scutata* Breb. B, *Coleochaete soluta* (Breb.) Pringsheim, showing zygotes in different stages of germination; *a*, *a*, zygotes from which swarm spores have escaped; *b*, *b*, zygotes containing nearly mature swarm spores. C, young plant of *C*, *soluta*. (From Pringsheim.)

Asexual reproduction is accomplished by large biciliate swarm spores.

Sexual Reproduction.—The antheridia are short, flask-shaped cells, and each bears a sperm having two cilia (Fig. 105, A, *s*). The oögonium is a flask-shaped cell with a long, slender neck that opens at the distal end (Fig. 105, B, *b* and C, *c*). After fecundation the basal part of the oögonium becomes surrounded by a cortex of cells developed near its base (Fig. 105, D).

On germination, after a period of dormancy lasting over winter, the zygote gives rise to a structure of 16 to 32 cells, each of which produces a swarm spore (Fig. 105, B, *b*). On being set free, the swarm spores give rise to new plants.

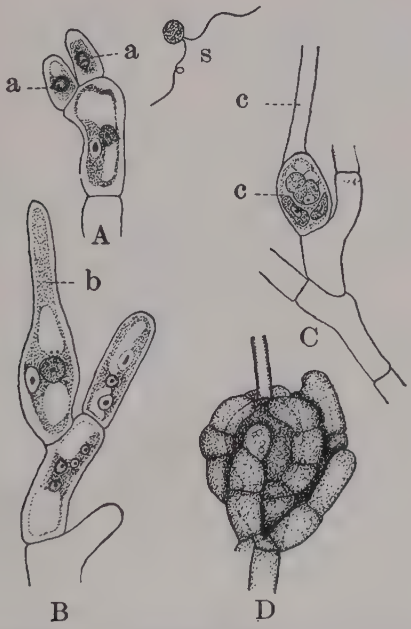

FIG. 105.—Fertilization in *Coleochaete pulvinata* A. Br. A, cell bearing two antheridia, *a a*; *s*, sperm. B, portion of branch bearing oögonium, *b*; C, *c*, oögonium in which egg and sperm nuclei are fusing; D, oögonium with cortical cells growing up about it. (A, B, C, adapted from Oltmanns; D, from Pringsheim.)

The cell structure developed from the zygote bears a resemblance to the diploid structure of a simple liverwort like Riccia. In the liverwort, however, the diploid structure has a wall of vegetative cells, and from each spore-bearing cell within, a tetrad of non-motile spores is produced. The covering about the zygote in Coleochaete is developed, as stated above, from adjacent vegetative cells. The reduction in the number of chromosomes from the double to the single number in Coleochaete occurs in the first nuclear division in the germinating zygote, so that the swarm spores resulting from the zygote constitute the beginning of the haploid structure.

Coleochaete soluta, as shown in Fig. 104, B, suggests a simple liverwort, containing diploid structures in different stages of development.

SIPHONALES—GREEN FELTS

The Siphonales include a large number of green algae presenting a wide diversity in size, form, general appearance, and habitat. They are common in both fresh and salt water, the larger and more complex plants living preferably in the warm seas. In structure all are generally similar in one respect; namely, the plant consists of a tubular, multinucleate cell or a number of tubular cells woven or grown together in a more or less compact mass.

Vegetative propagation occurs in a number of species. Asexual reproduction is accomplished by swarm spores. In the smaller forms sexual reproduction is brought about by motile isogametes; in the highest forms both sex organs and gametes are highly differentiated.

Vaucheria.—As a concrete illustration we shall select a species of Vaucheria such as *V. sessilis* or *V. geminata*. These plants grow on moist, shaded earth, or attached to stones or other objects over which cool, clear water flows. The latter often forms floating masses.

As shown in Fig. 106, A, the plant is a tubular, branched filament, containing many small, rounded chloroplasts and numerous small nuclei, which are visible only when stained. Oil drops are present among the chloroplasts. The normally developed filaments are without cross walls except where reproductive structures are formed, and where the filament has suffered some injury. The filament may, therefore, be regarded as a multinucleate cell (coenocyte). The species that grow on moist earth are attached to the soil by means of branched *rhizoids* (Fig. 106, G). A rhizoid serves as an organ for the absorption of water from the soil as well as for a holdfast.

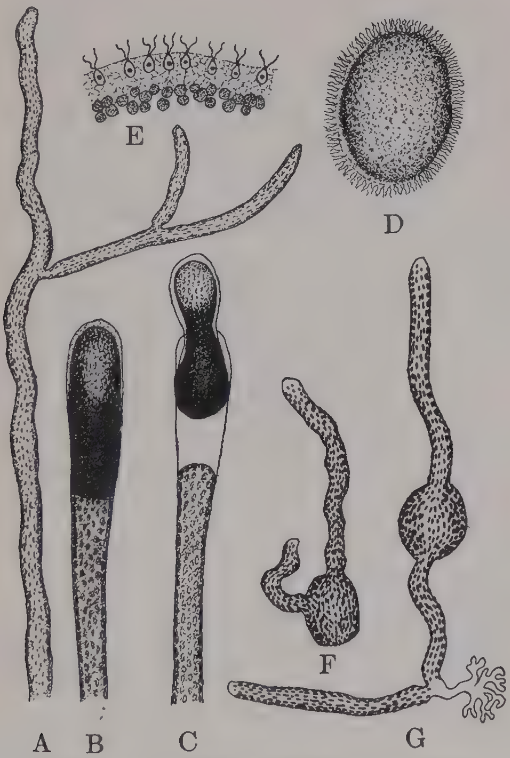

FIG. 106.—Vaucheria. Vegetative structure and asexual reproduction. A, portion of a filament of *Vaucheria sessilis*, showing mode of branching; B, C, D, *Vaucheria Ungeri* Nob.; B, end of filament forming sporangium; C, swarm spore escaping from sporangium; D, swarm spore killed with iodine, showing cilia; E, F, G, *Vaucheria sessilis;* E, peripheral portion of swarm spore stained to show relation of cilia to nuclei; F, germinating swarm spore; G, young plant developed from swarm spore. (B, C, D, from Thuret; E, from Strasburger; F, G, from Sachs.)

Asexual Reproduction.—Species that grow on moist soil, such as *Vaucheria repens* Hassall, or *V. sessilis*

(Vaucher) De Candolle, may develop swarm spores readily under experimental conditions. A thin layer of soil covered with a turf of the filaments is kept in the light in a moist chamber for a few days until numerous ends of filaments have assumed an upright position. The plants still attached to the soil, are then completely submerged in water and placed in the dark. In 12 to 24 hours, swarm spores will be formed. In the formation of the sporangium, the end of the filament becomes somewhat club-shaped, and of a dark green color, owing to the accumulation of chloroplasts and denser cytoplasm (Fig. 106, B). Many nuclei also migrate into the end of the filament. A cross wall is next formed, separating the end from the rest of the filament. This cell, which is now the sporangium, opens at the tip, and the entire contents escape as a globular or oval swarm spore with numerous pairs of cilia distributed over its entire surface (Fig. 106, B, C, D). Each pair of cilia corresponds to a nucleus, which is situated beneath the plasma membrane (Fig. 106, E). The swarm spore is, therefore, multinucleate. It is dark green in color, and after escaping from the sporangium moves slowly through the water for a short time. On coming to rest it germinates at once, sending out one or more slender tubes. If grown upon earth, the young plant may soon develop rhizoids (Fig. 106, F, G).

Sexual Reproduction.—To illustrate sexual reproduction *Vaucheria sessilis* or *V. geminata*, var. *racemosa*, may be selected. In *V. sessilis* the oögonia and antheridia may be formed near each other on the filament (Fig. 107, A). The antheridium, which is hooked or curved, is borne on a short pedicel. The numerous sperms produced in each antheridium escape through an opening in the distal end. The sperms are very small, somewhat pear-shaped, and provided with two laterally attached cilia (Fig. 107, C). The oögonium is sessile and obliquely oval. A rounded beak at the top indicates the place of opening. The oögonium bears a single large, uninucleate egg. The primordium of the oögonium is multinucleate,

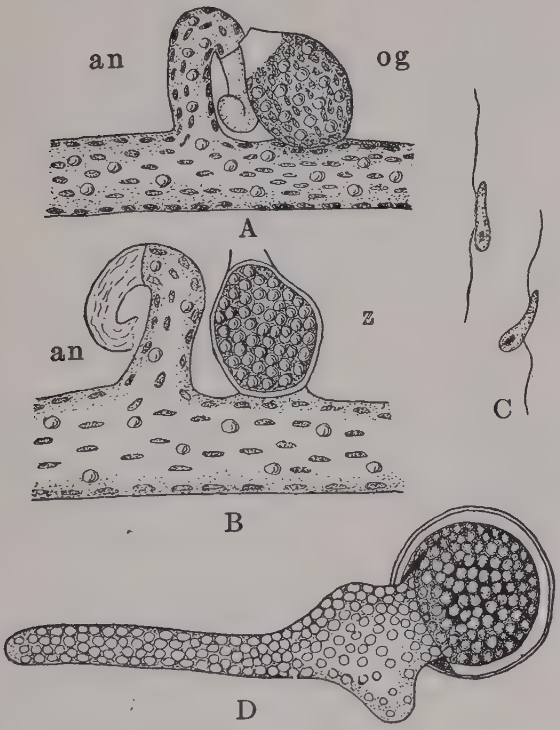

Fig. 107.—Sexual reproduction in Vaucheria. A, B, D. *Vaucheria sessilis* (Vauch.) D. C. A, portion of a filament bearing antheridium (*an*) and oögonium (*og*); B, later stage than A; *an*, empty antheridium; *z*, oögonium containing zygote; C, two sperms. D, germinating zygote. (Figures adapted: A, B, from Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers. C from Worowin; D from Pringsheim.)

but all except one of the nuclei either pass back into the filament before the wall separating the oögonium from the filament is formed, or they disintegrate. At the upper end of the egg, near the opening, is a colorless spot, the receptive spot.

After fecundation the zygote develops a thick cell wall, becomes dark brown in color, and passes into a dormant condition. On germination the zygote becomes green and grows directly into a new plant (Fig. 107, D).

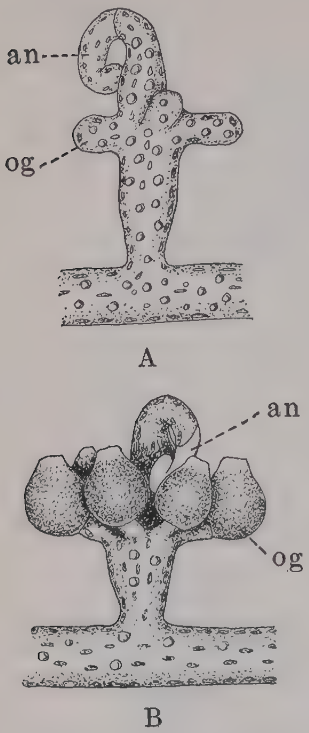

Fig. 108.—Formation of sexual organs in *Vaucheria geminata*, var. *racemosa* (Vauch.) Walz. A, the short side branch ending in the curved antheridium (*an*), below which are the beginnings of oögonia (*o*). B, mature sex organs. (Adapted from Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers.)

In *Vaucheria geminata*, var. *racemosa*, the antheridium and oögonia are borne upon a short side branch arising at right angles to the main filament (Fig. 108, A, B). This side branch ends in a more slender part making a ram's horn turn (Fig. 108, A). The terminal portion of the turn is cut off by a transverse wall to become the antheridium. As in *V. sessilis*, the antheridium is colorless and bears a number of sperms that escape through a terminal opening. Close below the base of the antheridium a number of oögonia are developed in a circle. Each is generally obliquely oval and is mounted on a short stalk (Fig. 108, B). It contains a single egg which is believed to have only one nucleus.

The zygote is doubtless the diploid structure, but as in the majority of fresh water algae, nothing is definitely known as to the time and place of the reduction division.

The Power of Healing Wounds.—Vaucheria, as well as many other members of the Siphonales, show a remarkable capacity to heal wounds when parts of the plant are cut or injured. When a filament of Vaucheria is cut in two by a sharp instrument, the cut ends may in fifteen minutes be closed by the formation of a cellulose wall. Masses of the contents that escape when a filament is severed may also become invested with a wall, especially if the escaped mass contains more than one nucleus. Filaments that are injured even slightly by pressure, or otherwise, will form a transverse septum at the point of injury. Or, if the injury be of greater extent in a linear direction, the entire injured portion may be divided off from the adjacent parts of the filament by cross walls. It is readily seen that this ability to repair injury or to heal wounds is of great value to the plant.

Botrydium.—*Botrydium granulatum* (L.) Grev. is a multinucleate, unicellular, terrestrial plant consisting of a deep green pear-shaped part above the ground, one to two millimeters in diameter, which tapers below to a narrower portion terminating in a system of much branched, colorless rhizoids that extend into the soil (Fig. 109, A). The part above the ground contains numerous small, rounded chloroplasts. The reserve food is in the form of an oil. Reproduction is effected by uniciliate swarm spores (Fig. 109, B, C, D).

The plant is common during the summer and early autumn on moist soil, along the edges of ponds, and in cultivated fields. Following rainy weather the plant may become so abundant on clay soil in corn fields as to impart a green cast to the ground.

Protosiphon.—Associated with Botrydium in the same habitat is *Protosiphon botryoides* (Küntz.) Klebs, a small, green, rounded or globular plant, which sends down into the soil a colorless, and generally unbranched, rhizoid-like part. The chloroplast consists, however, of a parietal, net-like layer, in which starch is present as

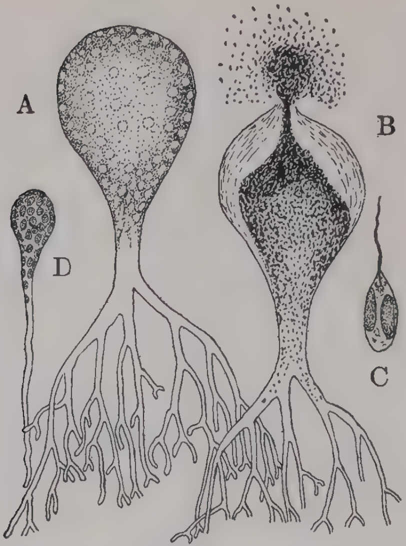

FIG. 109.—*Botrydium granulatum* (L.) Greville. A, an entire plant; B, plant producing swarm spores; C, swarm spore; D, young plant developed from a swarm spore. (Redrawn from Kny's chart.)

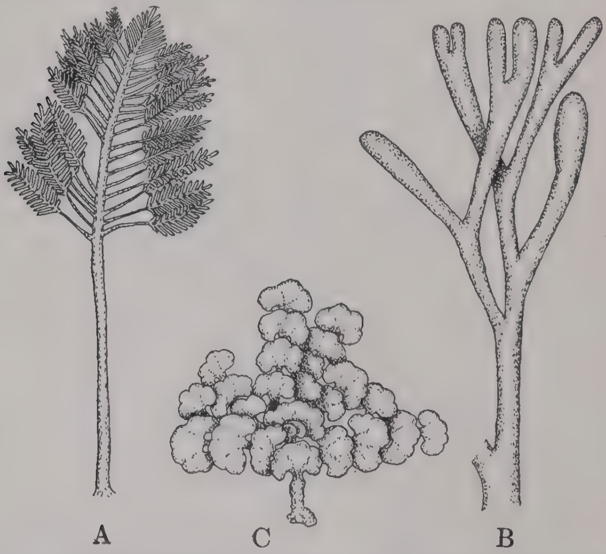

FIG. 110.—A, *Bryopsis plumosa*. B, portion of a plant of *Codium tomentosum*. C, *Halimeda opuntioides*. (A, modified from Thuret.)

a reserve food. The plant propagates vegetatively by division, the daughter cells sending down rhizoid-like prolongations.

Sexual reproduction is accomplished by biciliate gametes. When dried out or exposed to the sun, the cell contents separate into resting cells which become red in color. On being placed in water these develop biciliate gametes that unite to form star-shaped zygotes, which, after a period of rest, give rise directly to new plants. On moist earth the resting cells may develop directly into new plants. It is said that under some conditions the gametes do not unite but germinate directly.

Protosiphon is classed with the Protococcoideae by some authors.

The larger Siphonales, such as Bryopsis, Codium, Caulerpa, and Halimeda, are marine (Fig. 110, A, B, C).

Phyllosiphon.—A strange anomaly is presented by species of this genus which live as parasites within the tissues of leaves and stems of higher plants, as in the Jack-in-the-pulpit of our flora; in Europe the host is *Arisaema vulgare*, a plant related to our *Arisaema triphyllum*. Although the parasite does not penetrate the cells of the host, nor are specialized haustoria developed, it nevertheless ultimately exhausts the cells of the host.

CHARALES—STONEWORTS

Of the green algae, the Charales are the most highly differentiated. They are represented, in our flora, by two genera, Chara and Nitella, which are to be found submerged in lakes, ponds, and streams, attached to the soil by means of filamentous, much-branched rhizoids.

Chara.—A species of this genus will serve as an example. Chara consists of a slender axis composed of nodes (joints) and internodes (the part between the nodes) upon which are borne at each node a circle of dwarf branches (of limited growth), consisting also of nodes and internodes. These branches are sometimes spoken of as leaves. From the nodes of these dwarf branches are developed the so-called leaflets (Fig. 111, A, *b*). From the axil of one of the dwarf branches at each node there may arise a long branch or shoot (of unlimited growth), which repeats in every detail the

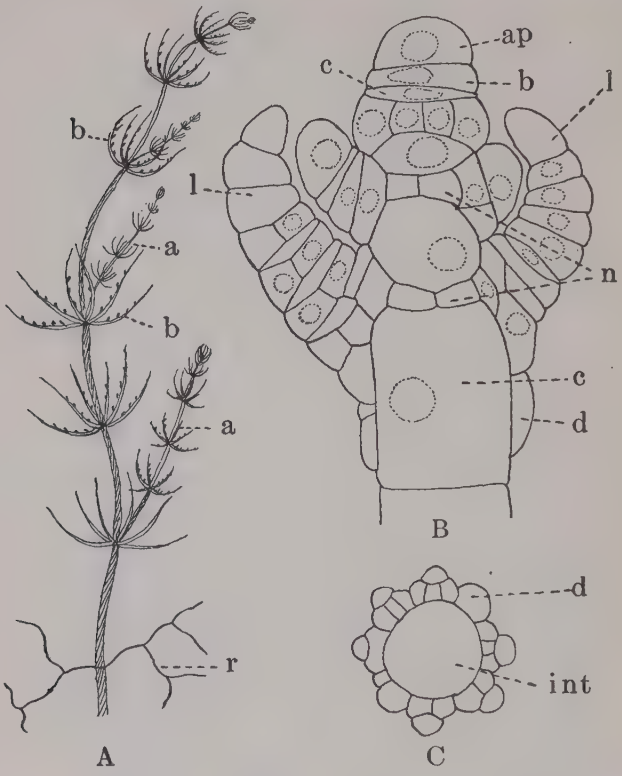

FIG. 111.—*Chara fragilis.* Habit and structure of certain vegetative parts. A, portion of plant showing long branches (*a*), dwarf branches (*b*), and rhizoids (*r*). B, longitudinal section through growing tip; *ap*, apical cell; *b*, nodal cell; *c*, internodal cell; *n*, node; *d*, cortical branch; *l*, leaf (dwarf branch). C, cross section of internode, showing internodal cell (*int*), and surrounding cortex (*d*). (Adapted from Campbell.)

structure of the main axis (Fig. 111, A, *a*). From one or more of the lower nodes are developed the multicellular, filamentous rhizoids. The sexual organs are borne at the nodes of the dwarf branches, the oval or elongated oögonium being above the globular antheridium. Frequently the plants are only a few centimeters in height, but they may attain a length of a meter or more. The surface of the older parts of the plant is often coated over with a deposit of lime, which accounts for the rough surface and brittle character of material that has been preserved in alcohol.

Growth and Structure.*—The main axes and branches grow from an apical cell, which in the long shoots is hemispherical in shape (Fig. 111, B, *ap*). From its base segments are cut off by transverse divisions. Each of these disk-shaped segments divides transversely into an upper cell (*b*), from which a node arises, and a lower (*c*), which gives rise to the central internodal cell. The latter is incapable of further division, but it increases enormously in size, extending the entire length of the internode. The upper segment, which elongates little if any, gives rise, by vertical divisions, to a node, ultimately consisting of a transverse disk of cells (*n*).

From the nodes all lateral members—dwarf shoots, long shoots, and rhizoids—are developed. The sex organs arise from the nodes of the dwarf branches (Fig. 112, A). Each central internodal cell is finally surrounded by a cellular cortex, consisting of strips or lobes, one-half of which grows downward from the upper node, and the other half coming upward from the lower node (Fig. 111, B, *d*). These two halves of the cortex meet in a zig-zag line about midway between the nodes. A cross section of an internode, as in Fig. 111, C, shows the relation of the central internodal cell and the surrounding cortex. The leaflets and terminal portions of the dwarf branches are not corticated. When a long branch is formed it takes the place of one of the upward-growing lobes of the cortex.

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* Only a brief description of details is given here.

The rhizoids grow also by means of apical cells. As stated above, they are formed from the lower nodes of the axis. The rhizoids are often spoken of as roots.

Vegetative Propagation.—Any mature node is capable of developing a shoot and rhizoids, thus producing a new plant. This may readily be demonstrated under experimental conditions by selecting a portion of the main axis consisting of two or more nodes and thrusting one of the nodes into the sand or soil in the bottom of the aquarium. Special bud-like structures are sometimes developed from the older nodes and on the rhizoids.

Sexual Reproduction.—The sex organs of the Charales are the largest and most complex among the algae. They spring from the nodes of the dwarf branches (Fig. 112, A). The mature oögonium of Chara consists of a large oval or elliptical egg surrounded by a cover of five tubular cells, which make two spiral turns around it. From the upper end of each of the tubular cells a short cell is cut off, the five constituting the crown of the oögonium (Fig. 112, B, *c*). When the egg is ready for fecundation the spirally twisted cells separate slightly below the crown, forming five clefts through which the sperms may enter.

The mature antheridium is globular in form and red in color, owing to a change of the green chloroplasts to red (Fig. 112, B, *an*). The vegetative framework of the antheridium consists of twenty-five cells. The eight triangular peripheral cells, four at each pole, are known as the "shields." The outer cell wall of each shield is marked by folds which radiate from the center and impart the very characteristic appearance to the surface of the antheridium. From the center of each shield there extends inward a large cylindrical cell, the *manubrium.* Each manubrium bears at its inner end a rounded cell, the *capitulum,* and each capitulum cuts off one or more secondary capitula. From the capitula grow out long, slender sperm-bearing filaments composed of numerous short cells. The four basal shields of the antheridium are attached to a large stalk-like cell which projects into the cavity of the antheridium, its inner end meeting the capitula (Fig. 113, *st*). Fig. 112, C represents one shield (*a*) with a manubrium (*b*) and its capitulum (*c*). Attached to the secondary capitula are a number of spermogenous filaments, *d*.

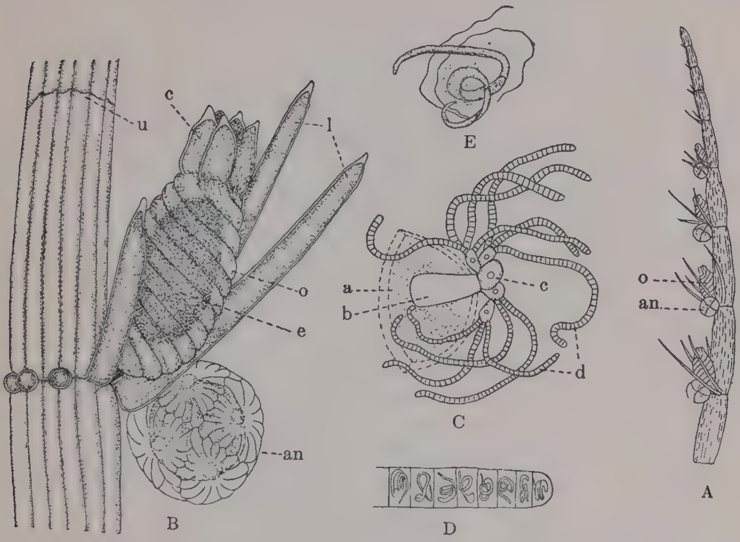

Fig. 112.—Sex organs of *Chara fragilis*. A, terminal portion of dwarf branch showing position of oögonia (*o*) and antheridia (*an*). B, node of dwarf branch with sex organs more highly magnified; *o*, oögonium; *c*, crown of oögonium; *e*, egg; *an*, surface view of antheridium; *l*, leaflets; *u*, line where ascending and descending cortical lobes meet. C, part of the antheridium as seen when the organ is carefully opened; *a*, a shield cell; *b*, manubrium; *c*, capitulum, to which are attached secondary capitula; *d*, sperm-bearing filaments. D, part of filament showing sperms in the cells. E, a sperm. (Figures adapted; A, from Strasburger; B, from Sachs; C and D, from Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers. E, from Mottier.)

The spermogenous filaments are coiled up in the spaces between the manubria (Fig. 113, *s*). From each cell of the filaments one sperm is formed. The sperm is a spirally coiled body, consisting of a nucleus and a specially differentiated part of the cytoplasm in the form of a thread or band. This differentiation, known as the *blepharoplast,* bears two long cilia (Fig. 112, E). The nucleus occupies the middle part of the sperm, while the blepharoplast extends its entire length. The posterior end of the blepharoplast is thicker and usually ends bluntly.

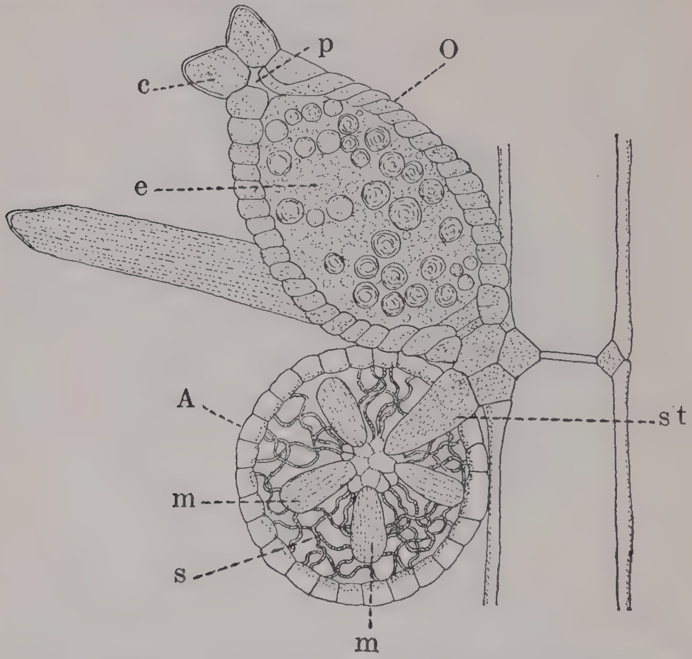

FIG. 113.—Chara. Longitudinal section of oögonium and antheridinm, with the node at which they are borne. O, oögonium; *e*, egg rich in stored food; *c*, crown; *p*, pore through which the sperm enters. A, antheridium; *st*, stalk cell of antheridium; *m*, manubria, extending from the center of eeac peripheral cell (shield) toward the center of the antheridium, and bearing at its inner end a rounded capitulum and secondary capitula; *s*, sperm-bearing filaments, borne by the secondary capitula. (Adapted from Strasburger.)

Fecundation, Zygote, and Proembryo.—When the antheridium is mature the shields separate and the sperm-bearing filaments are exposed to the water. Each sperm escapes through an opening in the wall of the

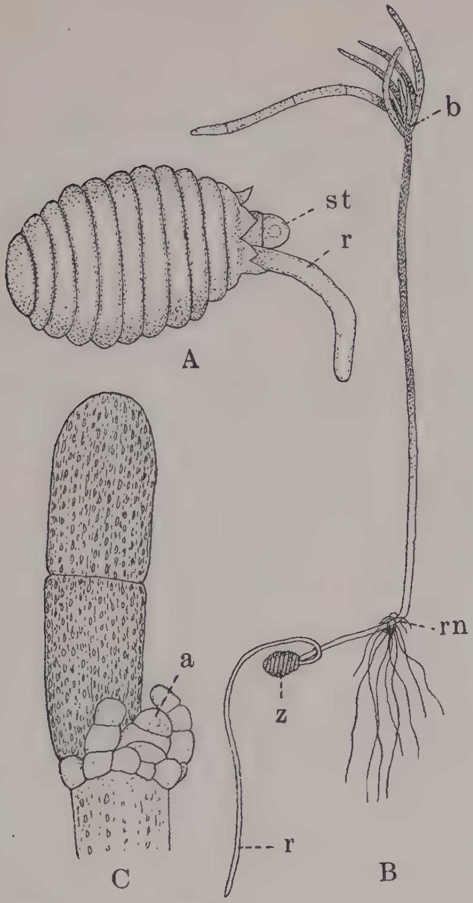

Fig. 114.—Chara. Germination of the zygote, and juvenile form (proembryo). A, germinating zygote; *r*, first root (rhizoid); *st*, apex of proembryo or juvenile form. B, proembryo; *c*, zygote; *r*, first root or rhizoid; *rn*, root node; *b*, node from which the adult shoot will arise as a lateral bud. C, distal end of proembryo; *a*, apical cell of lateral bud, from which adult form of plant develops. (A, C, from Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers. B, from Pringsheim.)

cell that bore it. The sperm enters the oögonium through one of the clefts beneath the crown and unites with the egg. The zygote passes into the resting stage and remains within the oögonium, which may become red in color. The oögonium with the enclosed zygote is a kind of fruit. It falls from the plant and sinks to the bottom of the pond or stream. The outer walls of the spiral cortical cells may decay, leaving the hardened inner walls standing out from the surface like the threads of a screw, (Fig. 114 A).

On germination the zygote produces first a small filamentous *proembryo*, a juvenile form of the Chara plant (Fig. 114, B). This proembryo consists of a primary rhizoid (*r*) and a small shoot having two nodes (*rn* and *b*). From the lower node rhizoids develop, and from the upper arises the adult form of the plant as a lateral bud (Fig. 114, C, *a*).

The diploid structure in Chara is the zygote. If the reduction division occurs during the germination of the zygote, the resulting Chara plant is the haploid structure.

In one species of Chara, *C. crinita*, it has been claimed for many years that the egg develops without fecundation, a phenomenon known as *parthenogenesis*. If the egg of this species possesses the single number of chromosomes, true parthenogenesis occurs, this being one of the few cases of such in the plant kingdom. But if the egg in this species contains the double number of chromosomes (no reduction having taken place), the phenomenon is not parthenogenesis, but *apogamy*.*

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* Parthenogenesis consists in the development of one gamete (here an egg) without union with another gamete. A gamete contains the single number of chromosomes. If the cell which seems to be an egg contains the double number of chromosomes, it is not a gamete; it cannot be fecundated, and its development constitutes what is properly known as *apogamy*. It may be reasonably questioned, therefore, whether such a thing as parthenogenesis occurs in the plant kingdom.

Nitella.—Another representative of the Charales commonly met with in our flora is Nitella. Having the same structural plan of nodes and internodes, it bears a striking resemblance to Chara. It differs from Chara in lacking a cortex, the large internodal cell being naked (Fig. 115, A). The oögonia and antheridia are similar to those of Chara, but the antheridium is borne above one or more oögonia, at the same node, and the crown is composed of ten cells in two tiers instead of one tier of five cells (Fig. 115, B).

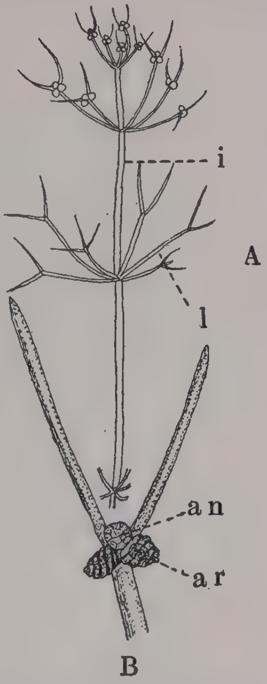

FIG. 115.—*Nitella flexilis.* A, a fertile branch; *i*, internode; *l*, leaves. B, leaf with two leaflets; *an* antheridium; *ar*, archegonium. (From Sachs.)

Mineral Deposit.—Chara often forms dense and extensive growths in the shallow water of ponds and lakes. During the winter most of the plant body dies, and the detritus resulting from decay and disintegration settle to the bottom. The limy incrustation and other mineral matter forms a deposit each year, and in some such manner our deposits of marl may have been built up in past ages.

CHAPTER XII

PHAEOPHYCEAE, BROWN ALGAE

The brown algae, the larger forms sometimes commonly called "kelps" or "rockweeds," are nearly all marine plants. They occur on all seacoasts, but attain their highest development in the cooler seas. They vary greatly in size, form, and structure, ranging from simple filaments to very large, massive structures with highly differentiated tissues. The giant kelp (*Macrocystis pyrifera*), which is the largest alga known to science, is said to attain a length of from 200 to 300 meters.

The characteristic brown color is due to the presence in the chloroplast of *fucoxanthin*, a pigment similar in chemical composition to xanthophyll. Brown algae vary in color from a deep brown to various shades of olive green; the characteristic pigment is always present, however. The large forms are of a tough, leathery texture, and are firmly anchored to the rocks or other objects by means of large holdfasts. Many are always submerged, but some, as in the case of Fucus, grow between high and low tides, so that the plant body is periodically exposed to the air at regular intervals.

There are three well defined larger subdivisions of the brown algae: Phaeosporales (Phaeosporeae), Fucales (Cystosporeae), and Dictyotales. As an example for more detailed presentation we shall select a species of Fucus.

FUCALES

FUCUS

Form and Structure.—The thallus, or plant body, consists of a flat, leathery, ribbon-like, dark brown structure traversed by a midrib. This is continued downwards into a rounded and somewhat cylindrical stalk, which ends below in an organ of attachment, the holdfast (Fig. 116, A, *h*). The branching is dichotomous. Here and there may be present large inflations, air

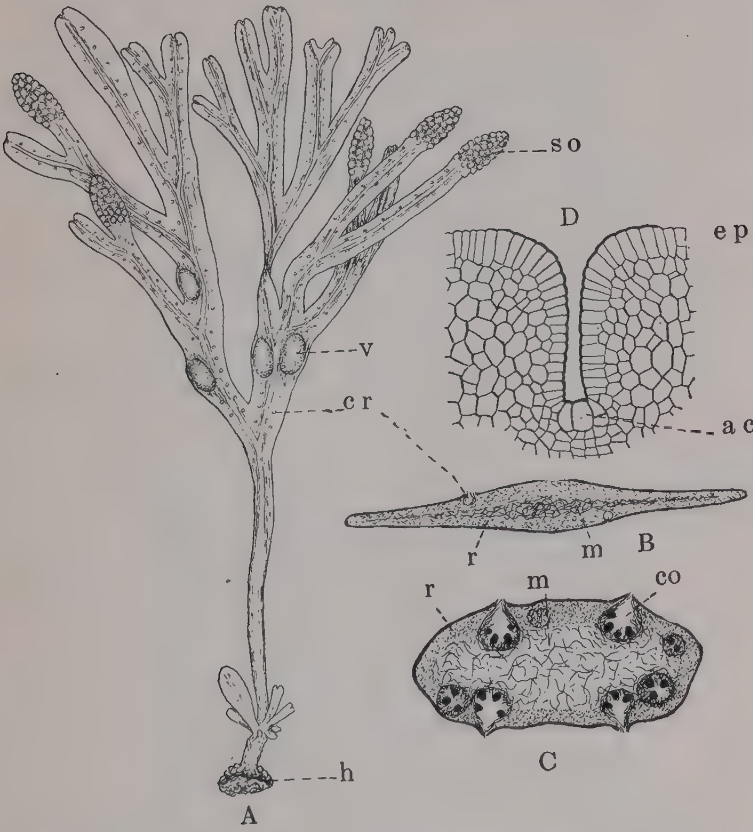

FIG. 116.—Fucus. A, portion of plant showing habit; *h*, holdfast; *v*, air vesicle; *so*, thickened fruiting ends bearing sex organs; *cr*, cryptostoma. B, diagram of cross section of thallus; *r*, outer rind; *m*, loose inner pith, or medulla; *cr*, cryptostoma. C, cross section of a fruiting tip; *con*, conceptacle, in which sex organs are borne. D, longitudinal section of a growing point taken at right angles to the flat surface, showing the pit, or depression, at the bot tom of which is the apical cell (*ac*); *ep*, epidermis. (D, from Kny's chart.)

vesicles, which help buoy up the plant in the water. These are sometimes grouped in pairs. Scattered over the flattened part of the plant, on both sides of the midrib, are numerous small dots (Fig. 116, A, *cr*). At the center of each dot is a pore, which leads into a cavity known as a *cryptostoma* (Fig. 116, B, *cr*).

In specimens bearing sex organs the ends of certain branches are enlarged and marked by numerous conical protuberances (Fig. 116, A, *so*). In the center of each protuberance is a small pore leading into a relatively large flash-shaped cavity, the *conceptacle*, in which one or both kinds of sex organs are present.

In cross section, the structure of the thallus is seen to consist of a firm rind, and a soft pith or medulla (Fig. 116, B). The rind is made up of small, closely arranged, isodiametric cells. The outer layer of these, which can be traced quite to the growing point, is the epidermis. The pith is composed of large cylindrical cells so placed together as to form a sort of network (Fig. 116, B, and Fig. 117). A copious mucilaginous substance present throughout the plant is derived from the outer surfaces of the cell walls.

Apical Growth.—The growing point of each branch of the thallus ends in an apical cell, somewhat rectangular in section, situated in a small depression at the tip of the branch (Fig. 116, D, *ac*). From this apical cell all other parts of the branch are primarily derived. The successive divisions of the apical cell take place in such way that cells are cut off from the four lateral faces and from the inner, or posterior, end. The true epidermis and other parts of the thallus can readily be traced to the apical cell (Fig. 116, D, *ep*). When the growing point branches this is due to a division of the apical cell into two nearly equal cells, each of which becomes the apical cell of a new branch. Dichotomous branching, which is so characteristic of Fucus, arises in this manner.

Reproduction.—Asexual reproduction by means of spores is unknown in the Fucaceae. Some of the Fucaceae, such as *Fucus vesiculosus* and species of Halidrys, are dioecious; others, such as *Fucus fastigiatus*, are monoecious. The oögonia are borne in rounded or flask-shaped cavities, *conceptacles*, aggregated at enlarged club-shaped ends, as in Fucus, or on special branches as in Sargassum (Fig. 120, *so*).

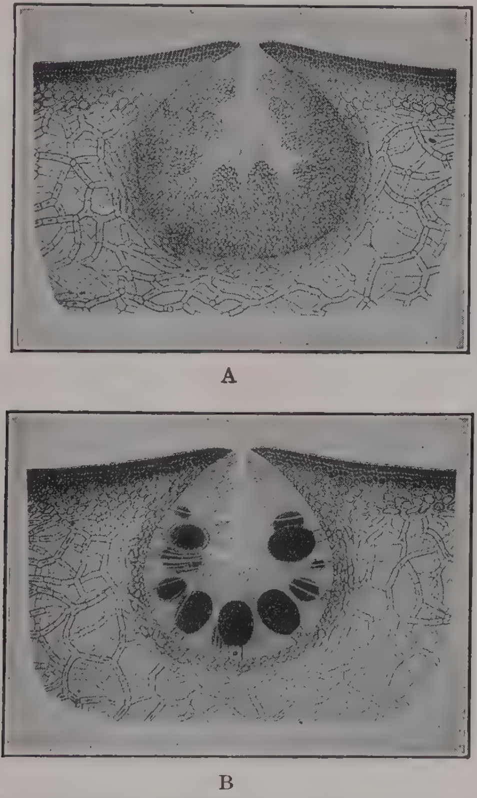

Fig. 117.—*Fucus vesiculosus.* Vertical sections through male (A) and female (B) conceptacles. (From Kny's chart, after Thuret.)

Antheridium.—Fig. 117, A, represents a male conceptacle. The antheridia (Fig. 118, *d*) are small oval or rounded cells borne at the ends of short branches arising from the inner wall of the conceptacle. At first the antheridium is a single cell. Its nucleus undergoes many repeated divisions, and finally cell division takes place, resulting in a large number of naked, biciliate cells, the sperms. When mature, the sperms are discharged into the water. Each is a pear-shaped cell provided with two laterally inserted cilia, one longer

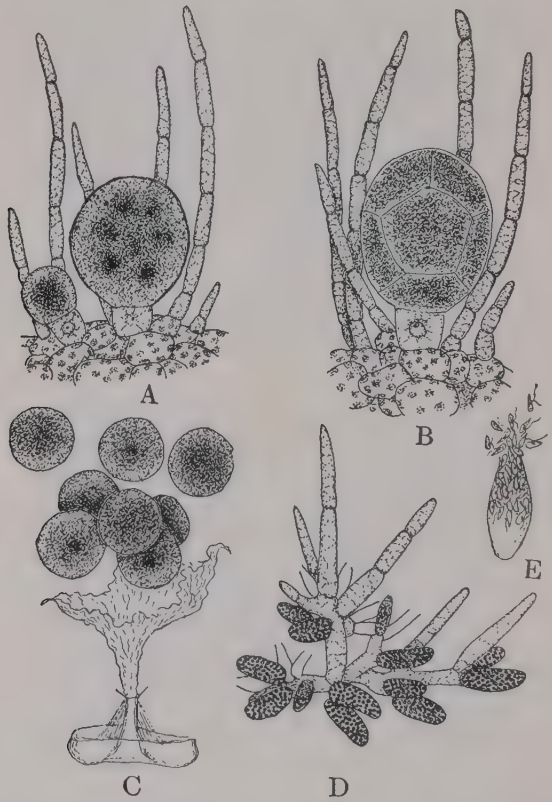

Fig. 118.—Sex organs of *Fucus vesiculosus.* A, two stages in the development of the oögonium. B, oögonium in which the eight eggs have been formed. C, eggs escaping from an oögonium. D, branched filaments from the male conceptacle, bearing antheridia. E, mature antheridium with sperms escaping. (From Thuret.)

than the other, and an orange-red pigment spot (Fig. 118, E).

Oögonium.—Fig. 117, B represents a female conceptacle. The oögonia arise also on short branches from the inner wall of the conceptacle. The young organ consists of a short basal stalk cell and a large terminal cell which bears the eggs. By three successive divisions the nucleus of this cell gives rise to eight nuclei, and the cell then divides into eight eggs (Fig. 118, A, B). At maturity the wall of the oögonium is dissolved, and the dark brown, non-motile eggs are discharged through the ostiole into the water (C).

Fecundation.—Certain phenomena of fecundation may be readily observed at the seaside laboratory. Fruiting ends of branches from which the gametes are being discharged are placed in dishes of sea water, the male and female branches being kept in separate dishes. If the eggs and sperms are properly brought together in a dish, or in a suitable mount for microscopic observation, some of the eggs will soon be seen rolling slowly through the water. Numerous sperms attach themselves to the surface of the egg. Each attaches itself by one cilium, while the other lashes the water. By this means each sperm maintains a circular or gyratory motion about its point of attachment. The movement is in the clockwise direction. By the combined action of all the sperms the egg is rolled slowly through the water (Fig. 119, A). Very soon a sperm enters the egg, and all the other sperms depart. The sperm and egg nuclei unite in a short time, and the zygote begins to grow without a period of rest. In the development of the new plant, the zygote divides into two cells, the lower one giving rise to the holdfast and the upper to the body of the plant (Fig. 119, B, C).

Haploid and Diploid Structures.—It has been found that the first mitosis in the oögonium of Fucus is a reducing division. It is assumed that a reducing division takes place also in the development of the antheridium. Eggs and sperms have the single number of chromosomes, and they alone represent the haploid structure, while the Fucus plant, whose cells have the double number of chromosomes, is the diploid structure.

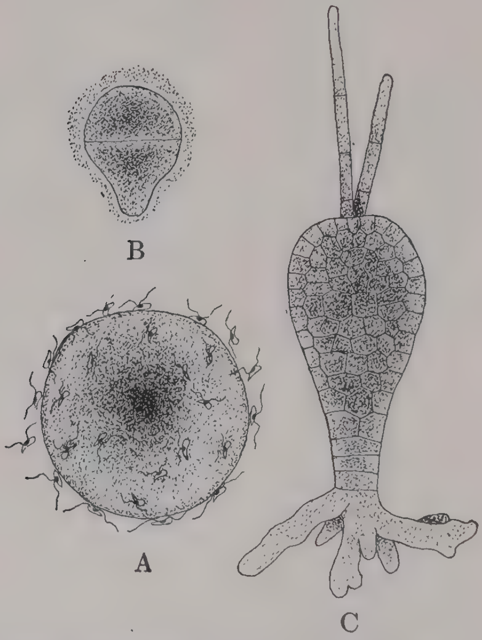

Fig. 119.—*Fucus vesiculosus.* A, egg to which sperms are attached. B, germinating zygote. C, young plant developing from zygote. (From Thuret.)

Among other Fucales may be mentioned Sargassum, Halidrys, Ascophyllum, etc. Sargassum is usually found floating in extensive areas in certain parts of the ocean far from the land, and because of this fact the plant constitutes the characteristic feature of the Sargasso Sea. These floating masses of seaweed serve as a shelter for a great variety of marine animals, small fishes even being found among them.

In certain Fucales fewer than eight eggs are formed in the oögonium. In Halidrys one egg is developed; in other genera two or four are formed. In all forms that have been carefully studied eight nuclei are present in the oögonium although eight eggs may not be developed.

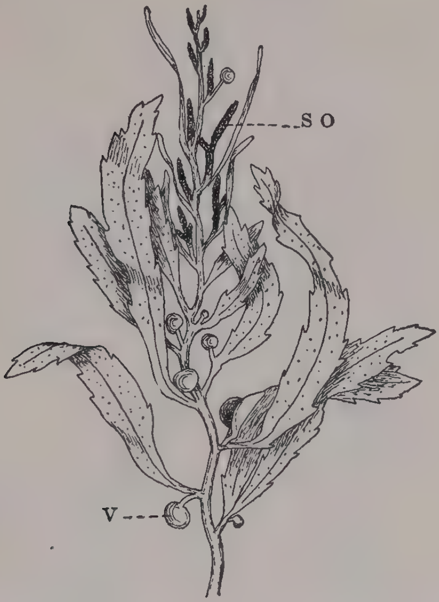

FIG. 120.—Sargassum. *v*, air vesicles; *so*, fruiting tips containing sex organs. × 1.

PHAEOSPORALES

Among the Phaeosporales are included some of the smallest and simplest Brown Algae, as well as the largest and most complex.

One of the best known simpler forms is Ectocarpus, which consists of simple branched filaments (Fig. 121, A). The large forms are represented by Macrocystis, Postelsia (the Sea Palm), and Laminaria (Fig. 123, A), along with numerous others.

Asexual Reproduction.—To illustrate both sexual and asexual reproduction in this group we may select *Ectocarpus siliculosis.* Asexual reproduction is accomplished by swarm spores, which are pear-shaped cells, each bearing two laterally inserted cilia, an eye spot, and a chloroplast. They are borne in what have long been known as *unilocular sporangia* (Fig. 121, B *sp*). In such a sporangium, which consists of a single cell, the contents divide successively into numerous cells which

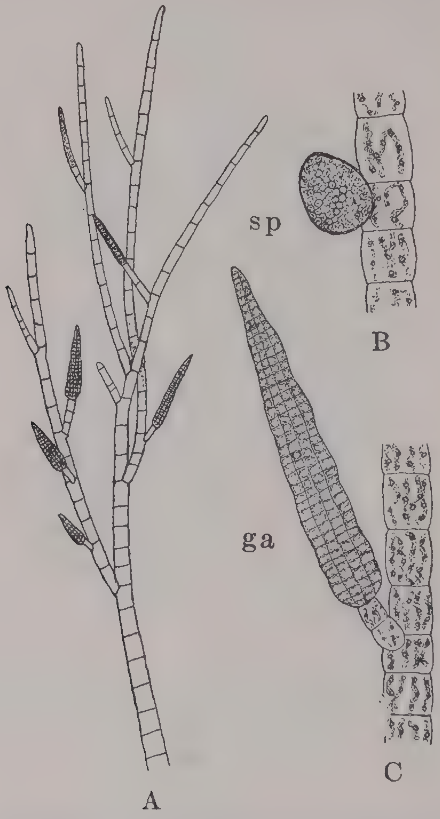

Fig. 121.—Ectocarpus. A, portion of plant showing habit. B, part of branch with a sporangium, *sp*. C, similar part of a plant with gametangium, *ga*.

are not separated by cell walls. These naked cells escape as swarm spores and develop directly into individual plants.

Sexual Reproduction.—Sexual reproduction is accomplished by motile gametes, which escape into the water and unite to produce zygotes. The gametes are similar in structure to the swarm spores, though smaller. They are formed in the so-called *plurilocular sporangia*, which in reality are gametangia (Fig. 121, C, *ga*). The initial cell of a gametangium divides into numerous small, cubical cells, which are separated by cell walls. The contents of each of these cells forms a motile gamete, which escapes into the water. In some species the gametes are unequal in size, the larger being eggs, and

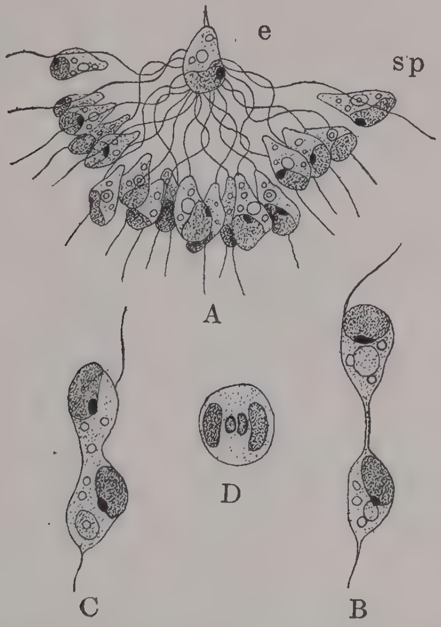

FIG. 122.—Union of gametes in *Ectocarpus siliculosis*. A, egg, *e*, to which are attached a large number of sperms, *sp*. B, C, egg and one sperm uniting. D, zygote just before fusion of the nuclei, which are lying side by side. (From Berthold and Oltmanns.)

the smaller, the sperms. It is also probable that the two sorts of gametes are borne in different gametangia. In fecundation, when observed in a hanging drop, the female gamete, as a rule, comes to rest first, and a number of sperms assemble about it. The sperms attach themselves by means of the longer cilium, as shown in the familiar illustration of Berthold (Fig. 122, A). One of the sperms now approaches the egg by a

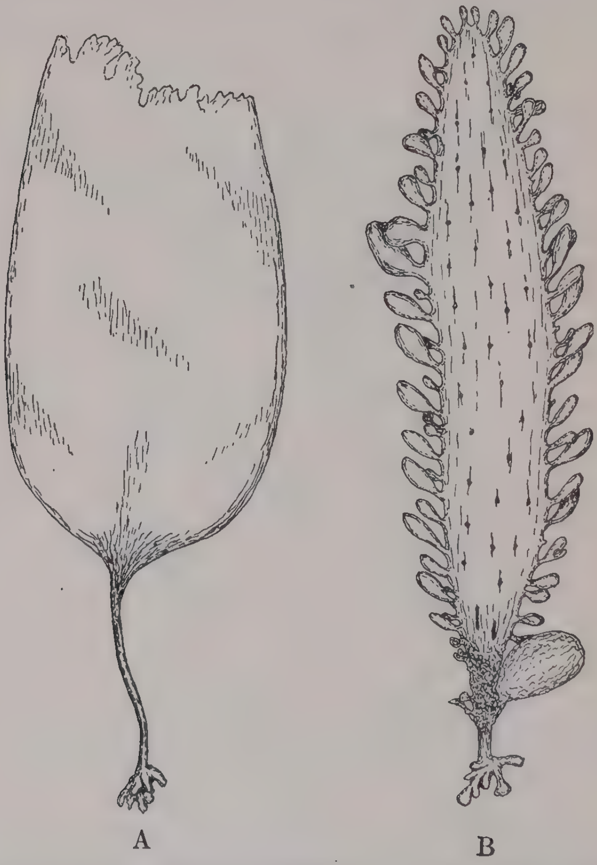

Fig. 123.—A, a small plant of Laminaria. B, a young plant of *Egregia Menziesii* Aresch. (From specimens collected by W. R. Shaw, at Point Lobos, California. × ⅔.)

sudden contraction, and unites with it, while the others withdraw. The two gametes then fuse to form the zygote. The chloroplasts do not unite (Fig. 122, B, C, D). The zygote germinates directly to form a new plant.

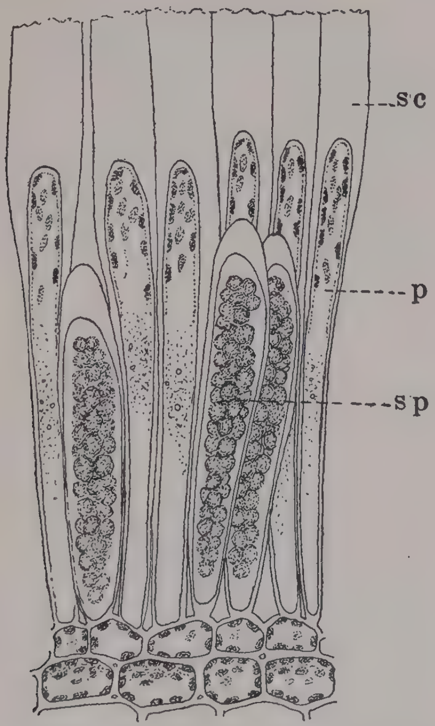

Fig. 124.—Section through a part of a sorus of *Laminaria saccharina*. *sp*, sporangium; *p*, paraphyses; *sc*, slime cap. (From Oltmanns; after Klebs.)

Haploid and Diploid Individuals.—For many years only the asexual form of reproduction was known in the large Phaeosporales, such as Laminaria, the sporangia being produced in large aggregations called *sori* (Fig. 124). In recent years it has been reported that these swarm spores do not develop into the large plant as we know it, but, on the contrary, give rise to very small, filamentous sexual plants, which are dioecious and bear very small antheridia and oögonia. The sperms and eggs escape into the water and form zygotes, which develop directly into the large structure known as Laminaria.

In Laminaria, and probably in other genera, therefore, the large massive plant producing swarmspores constitutes the diploid individual, while the small sexual plants mentioned are the haploid individuals. It is highly probable also that the plants bearing the swarm spores in Ectocarpus are the diploid individuals, and those producing the gametes are the haploid individuals. In these plants the number of chromosomes has not been determined.

DICTYOTALES

Because of its resemblance to certain red seaweeds in method of asexual reproduction, *Dictyota dichotoma* is of special interest. It consists of a small, dark brown, flat, ribbon-like plant, dichotomously branched (Fig. 125).

Asexual Reproduction.—It reproduces asexually by means of large, non-motile spores, termed *tetraspores*, because four are produced in a sporangium, a *tetrasporangium* (Fig. 126).

Sexual Reproduction.—This is accomplished by the union of highly differentiated eggs and sperms. The oögonia are produced in clusters, one egg to the oögonium (Fig. 127, A). The eggs are large, non-motile cells, which escape from the oögonia before fecundation. The sperms, which are motile, are produced in large numbers in antheridia, which are also aggregated in clusters (Fig. 127, B). As in Fucus, fecundation takes place in the open sea.

Haploid and Diploid Individuals.—It has been ascertained that the plant bearing tetraspores contains the double number of chromosomes, and that the reduction division takes place in the first nuclear division in the

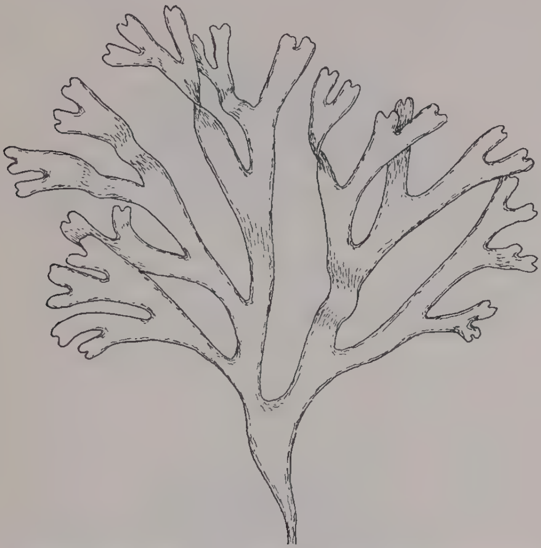

FIG. 125.—*Dictyota dichotoma*. Portion of plant showing mode of branching.

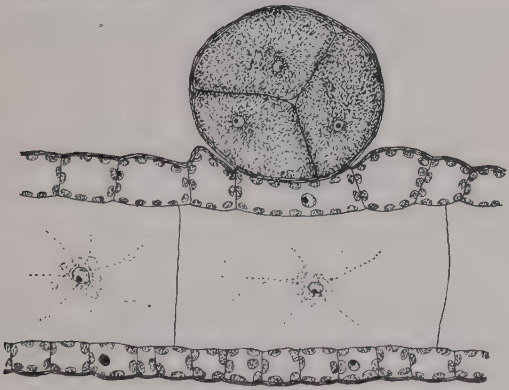

FIG. 126.—*Dictyota dichotoma*. Section of the thallus with tetrasporangium, showing three of the four spores.

tetrasporangium. The tetrasporic plants are therefore the diploid individuals. The plants bearing the antheridia and oögonia contain the single number of chromosomes; they are the haploid individuals. One complete life cycle of Dictyota embraces, therefore, two similar but separate and independent individuals, namely, the haploid, represented by the individual bearing eggs and sperms, and the diploid, by those that bear the tetraspores.

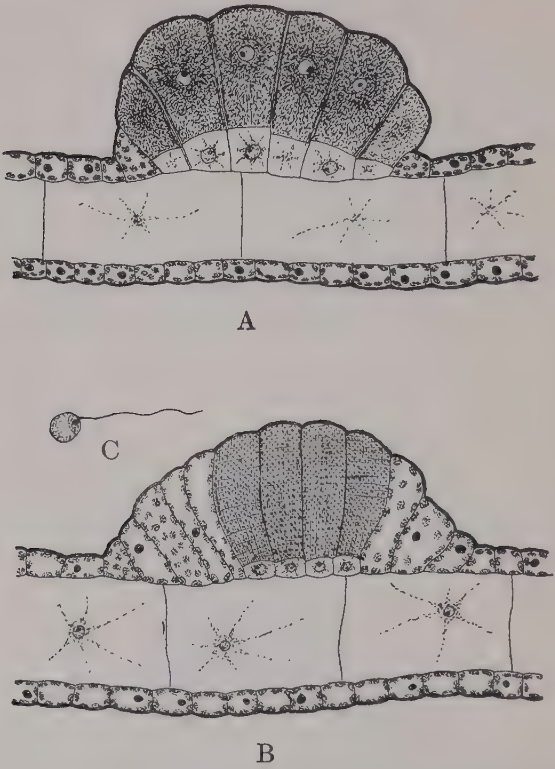

Fig. 127.—Sex organs of *Dictyota dichotoma*. A, sections of thallus with group of oögonia. B, group of antheridia. C, a sperm. (C, from Williams.)

CHAPTER XIII

RHODOPHYCEAE—RED ALGAE

The Red Algae owe their name to the characteristic red color possessed by the vast majority of the group. All are not red in color, however. Some, like Batrachospermum and Lemanea, for example, which occur in fresh water, are of a bluish green or dark olive green color. In marine forms, colors from a pale yellow to a dark purple occur. The bright red color is due to the presence of a red pigment, *phycoerythrin*, contained in the chloroplast along with chlorophyll. Phycoerythrin is soluble in rain water, imparting to the solution a rose-red color, which, owing to fluorescence, appears greenish yellow in reflected light.

In structure the Red Algae vary from delicate and almost microscopic filaments, branched or unbranched, to a larger, flat, and somewhat firm, leathery thallus. Some are strongly incrusted with lime, resembling coral-like structures (Corallina, Amphiora).

In the vast majority the chloroplasts are usually in the form of small oval disks, several in each cell. Generally the cell walls show a tendency to become gelatinous, and the intercellular gelatinous substance often becomes so great that the cells appear to be imbedded in it. As a rule, cytoplasmic connections extend from cell to cell.

The red pigment in the Red Algae and the brown in the Brown Algae seem to be associated with light as the source of energy in the process of photosynthesis.

Batrachospermum.—As an example for a more detailed consideration, we shall select Batrachospermum, which may be found in clear, cool streams in Indiana. The whole plant consists of a juvenile form, made up of simple, branched filaments, and the adult form, the Batrachospermum (Fig. 128, A). The adult form, or part, consists of an axial row of cells, ending in an apical

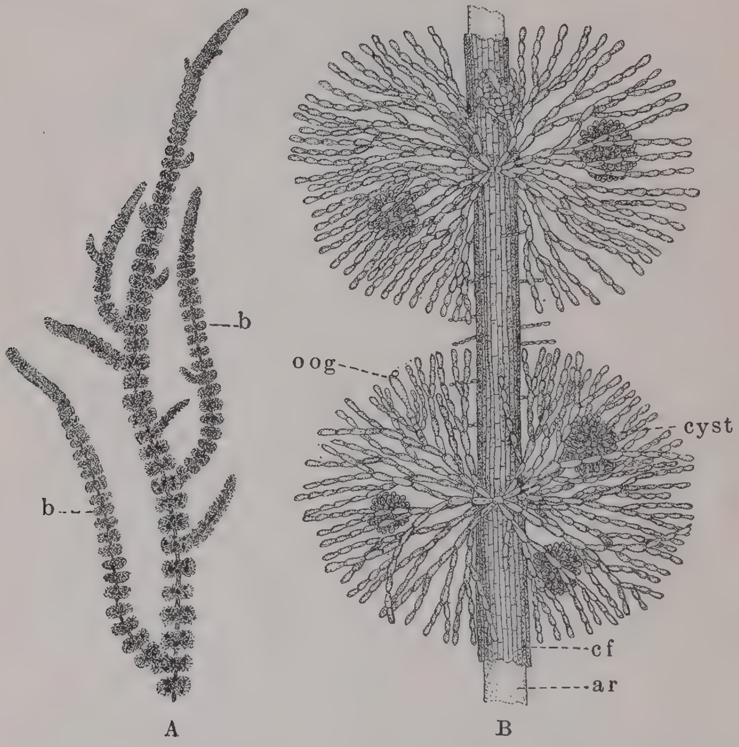

Fig. 128.—Batrachospermum. A, sketch showing habit of the plant. B, portion of long shoot with two glomerules of dwarf branches; *cyst*, cystocarp; oög, oögonium with sperm attached to tip of trichogyne; *ar*, axial row of cells; *cf*, cortical filaments.

cell, and a complex system of branches. From the upper end of each cell of the axial row is borne a whorl, or circle, of short branches of limited growth, composed of rounded or cylindrical cells constricted at the ends. Each branch bears some resemblance, therefore, to a row of beads or necklace. These dwarf branches are in turn branched, so that the whorl constitutes a dense glomerule. In fruiting specimens the spore fruits, *cystocarps*, appear, under low magnification, as dense, opaque masses among the branches of the glomerules. In the younger parts of the plant the whorls of branches are so close together that they conceal the central axis completely.

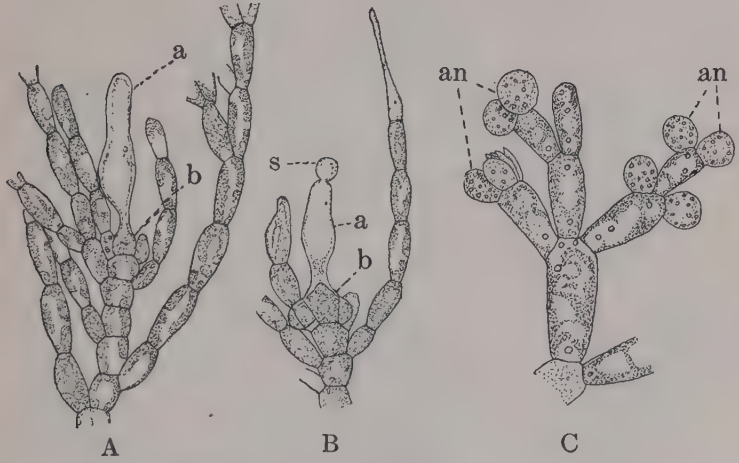

Fig. 129.—Sex organs of *Batrachospermum moniliforme.* A, part of a dwarf branch ending in an oögonium; *a*, the club-shaped terminal part, the *trichogyne; b*, the flask-shaped basal part, the *trichophore;* B, after fecundation, *s*, sperm attached to end of trichogyne. C, branch bearing antheridia (*an*). (A, B, from Strasburger.)

In addition to the dwarf branches, long branches are developed monopodially. These repeat in every detail the structure of the main axis (Fig. 128, A, *b*). The long branches, or shoots, arise from basal cells of the dwarf branches.

In older parts of the shoot the axial row of cells is covered by multicellular filaments, which may adhere laterally to form a sort of cortex. These cortical filaments spring also from the basal cells of the dwarf branches (Fig. 128, B, *cf*). In some species, slender branches spring from the cortical filaments, giving the axis between the glomerules a hairy appearance under a low magnification. The cells of the entire plant are covered with a coat of colorless slime.

Sexual Reproduction.—The antheridia consist of single cells borne at or near the distal ends of the branches of the glomerules (Fig. 129, C, *an*). Each bears a single non-motile sperm, which escapes into the water as a naked cell. The oögonia are borne at the ends of certain branches in the glomerules (Figl 129, A, *a*, *b*). Each is a single cell with a constriction near the lower end. The flask-shaped basal part is called the *trichophore* (*b*), and the larger, elongated, club-shaped terminal part is the *trichogyne* (*a*). The nucleus and cytoplasm in the basal part constitute the egg.

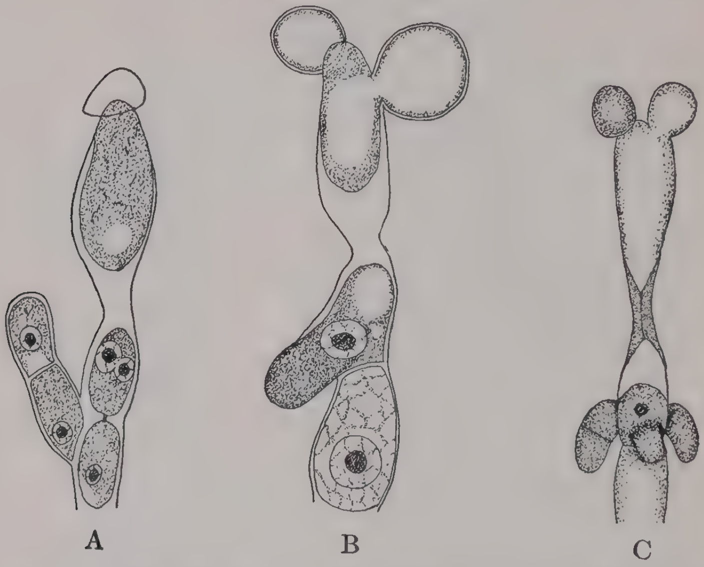

Fig. 130.—Batrachospermum. Fecundation and early stages in the formation of the cystocarp. A, fusion of egg and sperm nuclei in the trichophore. B, zygote germinating; beginning of the first sporogenous filament. C, three young sporogenous filaments sprouting out from the trichophore. (A and B, *B. boryanum*, after Osterhaut; C, *B. moniliforme*.)

Gravity and the movement of the water probably bring the sperm, or sperms, in contact with the end or side of the trichogyne, to which they adhere. When the sperms are found adhering to the trichogyne they possess a cell wall (Fig. 129, B, *s*). By dissolution of the cell walls an opening is formed between the sperm and the trichogyne. The contents of the sperm now pass into the trichogyne, and the opening in the latter is closed. The sperm nucleus passes down into the trichophore and fuses with the egg nucleus (Fig. 130, A).

The Cystocarp, or Spore Fruit.—The constriction between trichophore and trichogyne soon closes by a thickening of the cell wall. Neither the unfertilized egg nor the zygote rounds up or separates from the wall of the oögonium. The zygote begins germination at once. From it there grow out in all directions numerous short filaments, each of which ends in a spore, called a

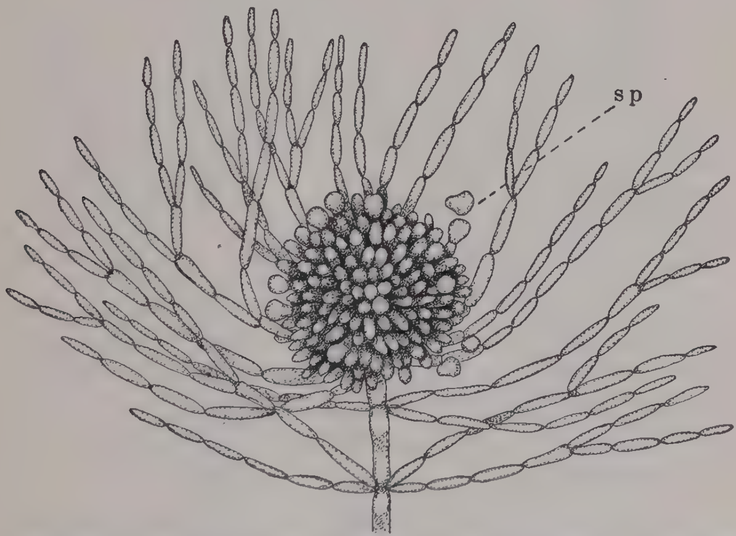

Fig. 131.—*Batrachospermum moniliforme.* Mature cystocarp. The cystocarp, borne at the end of a dwarf branch of the glomerule is surrounded by numerous secondary branches. *sp*, carpospores.

carpospore. These filaments are, therefore, spore-bearing, or *sporogenous*, filaments, and all together form a cystocarp (Fig. 131).

The sporogenous filaments are developed as follows: At one side of the trichophore after fecundation a bud-like protuberance is sent out. The nucleus of the zygote divides, one daughter nucleus remaining in the trichophore, the other passing into the protuberance, after which the division of the cell is completed (Fig. 130, B). This cell thus formed elongates and divides again, and the process is repeated until the completion of the sporogenous filament. The nucleus remaining in the trichophore again divides, and another sporogenous filament is produced as above described (Fig. 130, C). The process is continued until the entire cystocarp is developed. It will be seen that the nuclei of the sporogenous filaments and the carpospores are descendants of the nucleus of the zygote.

No asexual spores are produced on the adult form of Batrachospermum.

The Juvenile Form.—Presumably the juvenile form originates primarily from the carpospores. It consists of a much branched filament, resembling Cladophora in structural plan (Fig. 132). These filaments grow in dense tufts attached to blades of grass or other objects in the water. From this juvenile form, the adult part, the Batrachospermum, arises as a special branch.

The juvenile form develops asexual reproductive cells, or *monospores*, borne singly at the ends of short branches (Fig. 132, *sp*). In Fig. 133 is shown the manner in which the adult shoot, Batrachospermum, arises as a massive branch from the juvenile filament.

LEMANEA, as shown in Fig. 134, is a slender, tubular thallus with node-like enlargements at regular intervals. At each enlargement may be seen one or more openings through which the sperms enter. The oögonia are borne in the interior of the thallus, the antheridia on the exterior. Lemanea has also a filamentous juvenile stage.

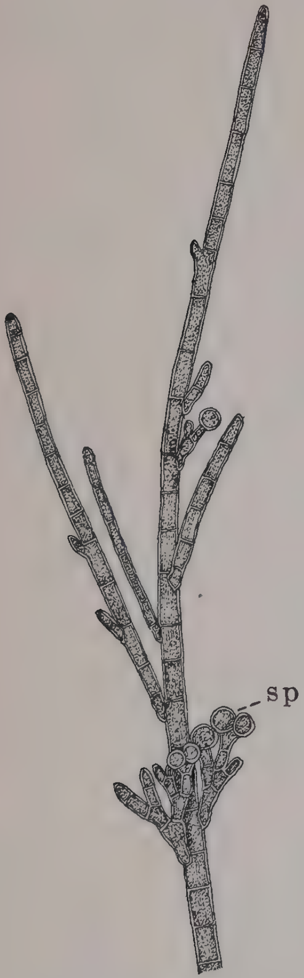

FIG. 132.—Branch of the juvenile form of Batrachospermum. *sp*, monospores.

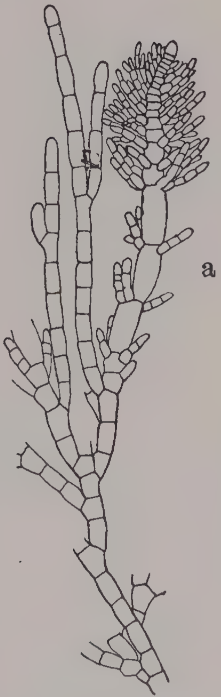

FIG. 133.—*Batrachospermum ectocarpum.* Juvenile branch with a young shoot of the adult form, *a*. (Adapted from Sirodot.)

Other Types of Red Algae.—As in Dictyota and certain Phaeosporeae, the complete life cycle of some of the

Red Algae is known to consist of two distinct individual plants. One of the individuals bears tetraspores, and is called the tetrasporic plant, or the diploid individual; the other bears cystocarps and carpospores; it is known as the haploid plant. The two plants may resemble each other closely.

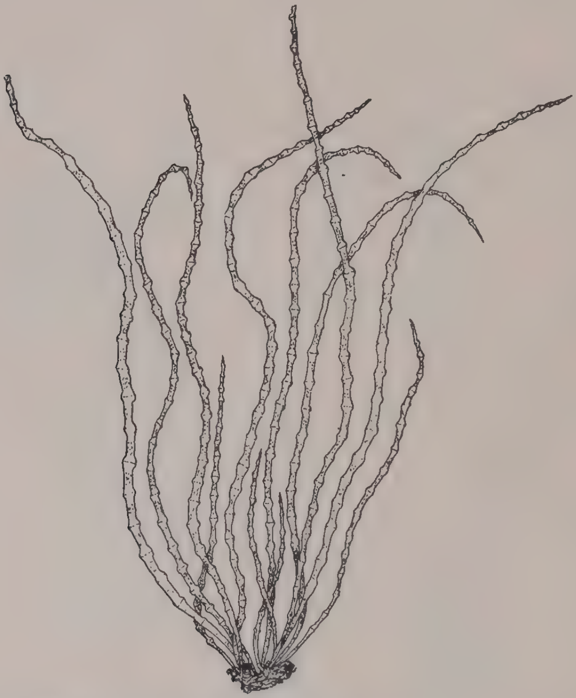

FIG. 134.—Lemanea. Several shoots attached to a bit of limestone. (Slightly enlarged.)

The above statement may be made clear by means of a concrete case, such as that afforded by Polysiphonia. Fig. 135, B represents a portion of the haploid plant bearing a cystocarp. Here the cystocarp is not naked as in Batrachospermum, but surrounded by an urn-shaped protective covering, provided with an opening at the top through which the carpospores escape. Apart from the covering, these cystocarps arise in a manner similar to that in Batrachospermum. Fig. 135, D, is the end of a branch bearing two antheridia, *a*, *a*. The

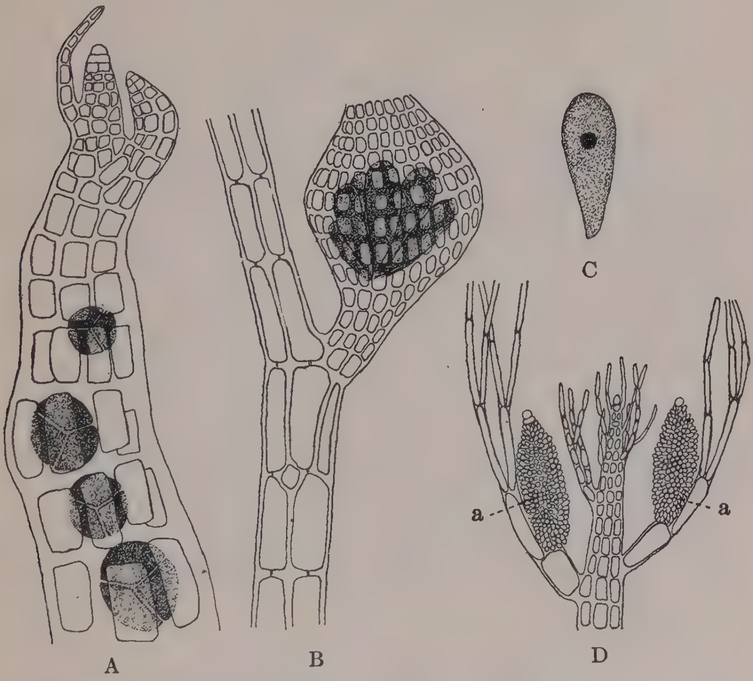

FIG. 135.—*Polysiphonia violacea.* A, tip end of tetrasporic plant, showing tetrasporangia, each with its four spores. B, portion of haploid plant bearing an urn-shaped cystocarp, enclosing the carpospores. C, a carpospore. D, branch with two antherida (*a*). (B, C, and D from Bergen and Davis' "Principles of Botany." By permission of Ginn & Company, Publishers.)

carpospores on germination give rise to the tetrasporic plant, a portion of which is shown in Fig. 135, A. The tetraspores, on germination, give rise, in turn, to the haploid individuals.

CHAPTER XIV

FUNGI

The fungi include a large assemblage of plants representing more than forty thousand known species. They are of about the same structural rank as the algae, but differ from the latter in the *absence of chlorophyll.*

Fungi are, therefore, incapable of making their own food, which must be secured from other organic bodies. When they secure food from living organisms, fungi are termed *parasites;* if the source of food be dead organic matter, the fungus is known as a *saprophyte.* Many fungi are able to live both as parasite and saprophyte.

For convenience and simplicity we shall speak of the fungi as embracing two great sub-divisions: the Phycomycetes (algo-fungi), and the Mycomycetes (Eumycetes), or true fungi.

PHYCOMYCETES (ALGO-FUNGI)

The Phycomycetes are called algo-fungi because of their resemblance in structure and reproduction to such algae as Vaucheria.

The mycelium consists generally of tubular, multinucleated filaments, which are without cross walls except where reproductive organs are formed; the mycelium of the Mycomycetes is septate. In some cases, however, the mycelium of the Phycomycetes may be septate.

Rhizopus.—As our first representative of the Phycomycetes we shall select a very common bread mould, *Rhizopus nigricans* (*Mucor stolonifer*), which will develop almost invariably upon bread kept in a moist, warm place, from spores that are in the air. If a piece of moist bread be exposed to the air for a few minutes, and kept in a warm place under a bell jar or other vessel, a crop of mould will develop in a day or two.

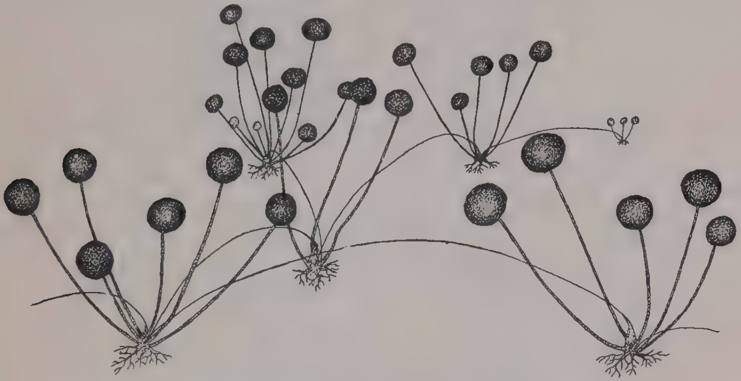

Fig. 136.—*Rhizopus nigricans.* Habit.

The Plant Body or Vegetative Mycelium.—The young plant of Rhizopus appears as a weft of fleecy white mycelium on the surface of the bread. Save in older plants, and where reproductive bodies are formed, the mycelium consists of branched tubular filaments* (Fig. 137). With age the walls of the hyphae turn dark or

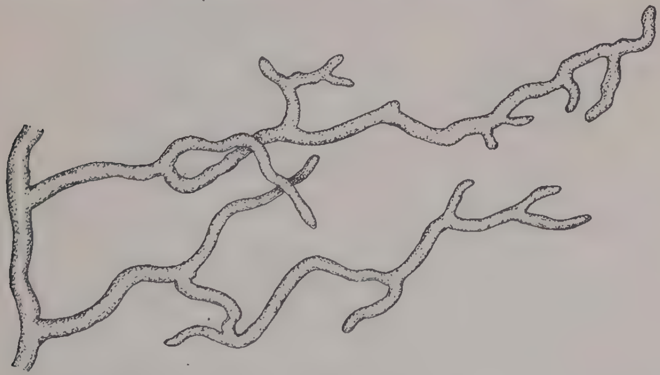

Fig. 137.—*Rhizopus nigricans.* Mycelium from inside the substratum.

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* A single filament is called a *hypha;* plural, *hyphae.*

smoky brown. Here and there hyphae are sent down into the nutrient substratum. From certain places in these hyphae, where rhizoid-like structures are developed, there arise two sorts of branches, *sporangiophores* and runners, or *stolons*. The stolons spread readily and extensively over the bread or other substratum, sending into or toward the substratum rhizoid-like branches, and into the air clusters of *sporangiophores* (Fig. 136).

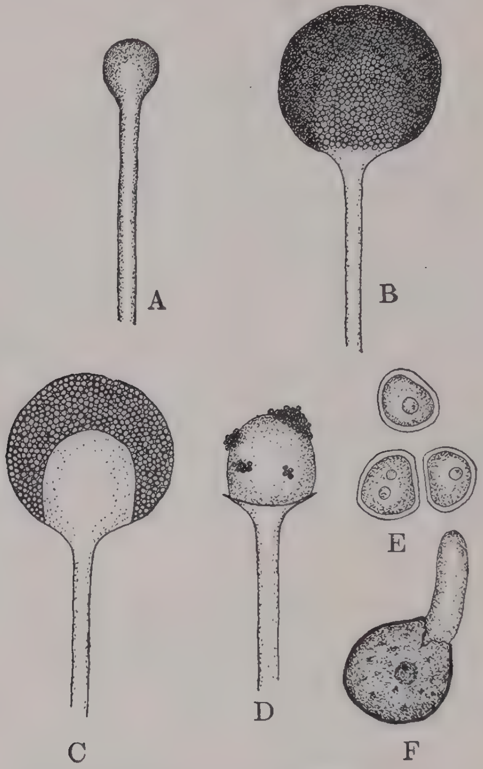

Fig. 138.—*Rhizopus nigricans.* The sporangium. A, a very young sporangium. B, sporangium almost mature. C, same as B, but in section, showing columella and spores. D, old columella with a few spores still attached. E, spores. F, germinating spore.

Asexual Reproduction.—Asexual reproduction is accomplished by spores borne in globular sporangia at the ends of stout upright hyphae, sporangiophores (Fig. 138, A-C). When mature the wall of the sporangium is very brittle, and is readily broken.

The sporangium arises as follows: The upper end of the young sporangiophore enlarges into a globular head, into which flows dense cytoplasm and many nuclei. The head or sporangium is now separated by an arched cross wall, the columella (Fig. 138, A, B, C). The contents of the sporangium, by progressive cleavage (See page 10), gives rise ultimately to numerous rounded spores with dark or smoky brown walls. Each spore contains one or more nuclei (Fig. 138, E, F).

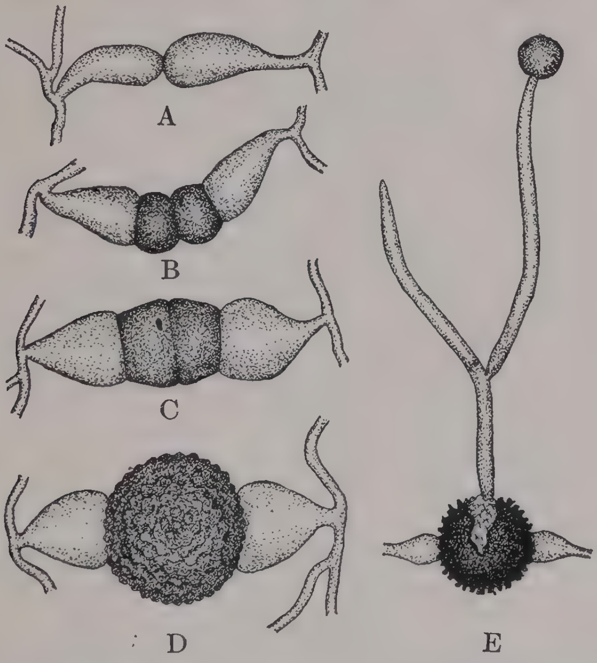

Fig. 139.—*Rhizopus nigricans.* Formation and germination of zygote. A-D, steps in conjugation, ending in the mature zygote. E, germination of zygote (Mucor). (E after Brefeld.)

Sexual Reproduction.—Rhizopus nigricans is dioecious, so that unless mycelia of the two sexes grow intermingled, zygotes will not be formed. In laboratory cultures, if mycelia of different sexes be grown side by side upon the culture medium so that the hyphae of one will intermingle or interlace with those of the other, a windrow of zygotes will appear along the line at which the mycelia meet and intermingle. If bits from the strip or windrow be examined, all stages in the formation of the zygotes may be seen.

The process is briefly as follows: Short, club-shaped branches from neighboring hyphae of opposite sex meet end to end (Fig. 139, A). These branches are gametophores. From the end of each of these a cell is cut off (B). These cells, which contain several nuclei, are the gametes. An opening is now formed between the two gametes, and the contents unite, the nuclei fusing in pairs. This phenomenon is known as multiple fecundation, or multiple fusion of gamete nuclei. The zygote soon reaches maturity, developing a thick, complex cell wall which is black or dark brown, and very rough or warty externally (C, D).

Germination of the Zygote.—After a period of dormancy, and on the return of favorable conditions, the zygote germinates, sending out a short hypha which develops a sporangium at its distal end (Fig. 139, E). The spores in this sporangium are the beginnings of new life cycles. Approximately one half of these spores are functionally of one sex, and one half of the opposite sex, the mycelium resulting from any one spore will, therefore, be functionally unisexual.

The Haploid and Diploid Structures.—The zygote and hypha resulting from its germination probably represent the diploid structure. If the reduction in the number of chromosomes takes place during or following the germination of the zygote, the spores in the sporangium of Fig. 139, E, and the mycelia resulting therefrom will represent the haploid structure.

Monoecious and Dioecious Mycelia.—A monoecious mycelium has two kinds of gametes, male and female. One mycelium represents, therefore, the complete haploid structure of a life-cycle. When the mycelium is dioecious, one individual mycelium bears one kind of gamete, and another mycelium the other kind of gamete. Under such circumstances there are two haploid individuals in a life cycle.*

When a monoecious mycelium propagates asexually by spores, all of the spores are functionally bisexual, and all the resulting mycelia will be monoecious. If a dioecious mycelium reproduces asexually by spores, the male mycelium will develop male spores, and male mycelia will always result. If the mycelium be female, only female mycelia will result from asexual reproduction.

Some species of moulds are monoecious. One mycelium constitutes the complete haploid structure in a life-cycle. The spores developed upon the hypha coming from the zygote, will be all of one kind, or bisexual, instead of two kinds as in the case of *Rhizopus nigricans*.

Pilobolus.—Belonging to the same group as Rhizopus is the interesting mould Pilobolus, which grows on dung of herbivorous animals. The stout sporangiophore has a large, bulbous expansion just below the sporangium (Fig. 140, A). This enlargement is a kind of explosive apparatus, or pop gun, by which the sporangia are expelled into the air, and also a sense organ by which the sporangiophore responds to the direction of light. If Pilobolus with maturing sporangia be placed in a dark chamber provided with a small window to admit light, it will be seen after a few hours that the window will be peppered over with the small, black sporangia, and that the sporangiophores will all be inclined toward the window (Fig. 141). The sporangiophore is positively phototropic, and the sensitive portion is in the bulbous swelling. It has been found that in some cases the sporangia have been thrown a distance of six feet in a horizontal direction. The sporangia adhere to the object against which they strike.

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* In recent literature the two mycelia are spoken of as + and −, the (+) mycelium representing the female, and the (−) representing the male. The (+) mycelium is usually more vigorous than the (−) mycelium. Dioecious species are now frequently referred to as *heterothallic*, while the monoecious forms are designated as *homothallic*.

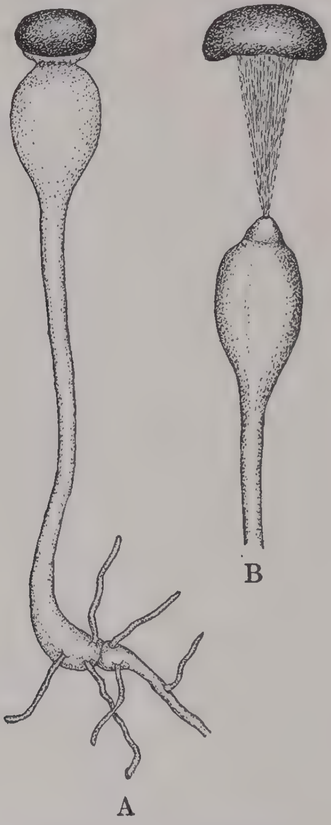

Fig. 140.—*Pilobolus crystallinus*. Sporangiophore. B, The Pilobolus "gun" in action. (A after Brefeld; B after Zopf, from Schenck.)

In nature Pilobolus grows on dung close to the ground. The sporangia are shot up into the air toward the light, striking blades and stems of grasses and other plants. The spores are said to grow readily only after having passed through the alimentary tract of herbivorous animals. The sporangia adhering to forage plants are eaten by the animals. The explosive discharge of the sporangia is, therefore, an ecological adaptation in the life of Pilobolus.

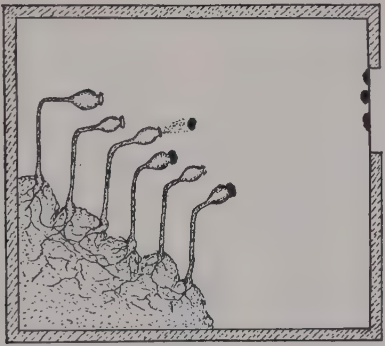

Fig. 141.—Pilobolus. Response of sporangiophore to light. A culture of the fungus is placed in a box, and light is admitted only through a small window. The sporangiophores bend toward the window, in response to the stimulus of light, and the sporangia are shot off forcibly against the window, to which they adhere.

Albugo.—As a second representative of the Phycomycetes we shall select for more detailed presentation the parasite *Albugo candida*, found in the spring on the Shepherd's Purse plant (*Capsella Bursa-pastoris*), and producing what is called the White Rust.

Vegetative Structure.—The plant body of Albugo consists of a system of tubular, branched, multinucleate filaments, which live within the intercellular spaces of the host plant. It is, therefore, an internal parasite. The manner in which it secures nourishment from the host cells will be explained in a later paragraph.

The presence of the parasite is recognized in its earlier stages as white pustules, or blisters, varying in size from that of a pin head to large white expansions covering longer stretches of the stem or leaves (Fig. 142, A). These pustules are caused by numerous colorless spores, *conidia,* developed in immense numbers just beneath the epidermis of the host. The conidia are the asexual reproductive bodies.

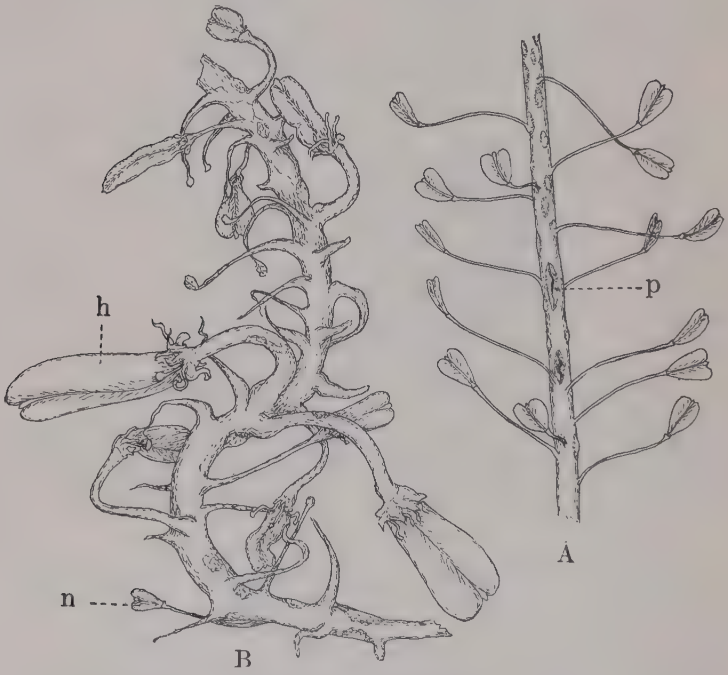

FIG. 142.—Stems of Shepherd's Purse affected with the White Rust (*Albugo candida*). A, stem of normal size showing pustules of conidia (*p*). B, portion of stem showing a later stage of the disease. The parasite causes the stem and seed pods to become greatly enlarged and distorted (hypertrophy); *n*, normal seed pod, about natural size; *h*, diseased seed pod showing hypertrophy. These enlarged diseased stems contain enormous numbers of zygotes of the fungus.

Asexual Reproduction.—A cross section of the stem or leaf of the host, passing through a pustule, will illustrate the manner in which the conidia are developed and how the pustule is formed (Fig. 143, A, B). In a pustule still covered by the epidermis the conidia will be seen in rows. Each chain may be traced back to an upright, club-shaped hypha, the *conidiophore* (Fig. 144, A). From the upper end of the conidiophore the conidia are abjointed singly, producing the row, the outermost one, next to the epidermis, being the oldest. The conidia are connected by narrow necks formed from the cell wall. The accumulation of conidia gradually pushes out the epidermis until it is finally ruptured and the conidia are set free. The masses of conidia appear to the naked eye as white flour. They are scattered by the wind.

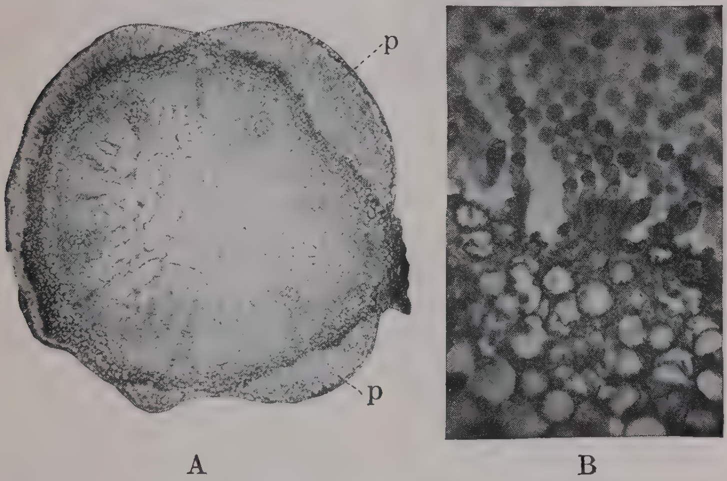

Fig. 143.—*Albugo candida.* A, cross section of infected stem of Capsella, showing blisters filled with conidia. B, Conidiophores with chains of conidia.

Germination of Conidia and Infection of the Host.—Under favorable conditions of moisture and temperature the conidia will germinate. Each contains about eight nuclei. The contents divide into eight cells, which escape as biciliate swarm spores (Fig. 144, B, C, D). The conidia are really sporangia. If the germination occurs on a suitable part of a host, as a young, tender portion, infection will take place. The swarm spores come to rest and germinate by sending out a germ tube (F). This germ tube penetrates the tissue, and the parasite is soon established within its host.

From the foregoing it is readily seen that the conidia are the means of rapid infection, the mycelium in one diseased host plant being sufficient to supply conidia to infect many other near-by plants. In exceptional cases the conidia are said to germinate by sending out a germ tube directly.

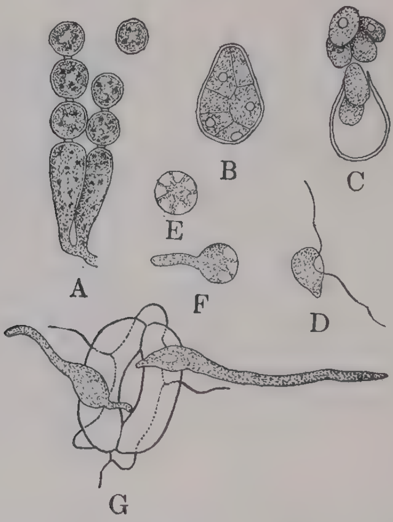

Fig. 144.—*Albugo candida.* Asexual reproduction. A, two conidiophores, each forming a chain of multinucleated conidia. B, a conidium which has produced within itself as many swarm spores as it had nuclei. C, swarm spores escaping from conidium. D, a swarm spore. E, a swarm spore which has come to rest and lost its cilia. F, G, swarm spores germinating and infection tubes entering stoma of the host. (B-G, from DeBary.)

Sexual Reproduction.—After a time conidia will cease to be developed on a given host, and some of its stems, leaves, and seed pods will appear of an abnormal size; i.e., over developed (hypertrophy) and of a dark or brownish color. If the stem of such plants be examined, numerous, yellowish or brown zygotes will be found distributed throughout its tissues (Fig. 146, A). Each zygote has a thick, brown wall of two or more layers, with irregular thickenings on the outside.

Oögonia and Antheridia.—The zygote is developed, of course, from the fecundated egg. The oögonia and antheridia arise from separate hyphae deeply seated

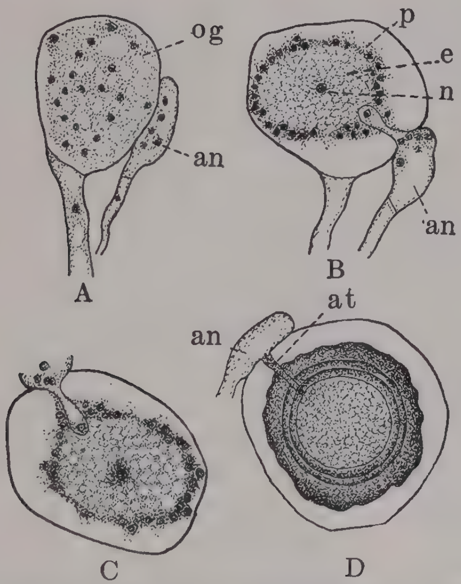

Fig. 145.—*Albugo candida.* Sexual reproduction. A, young oögonium (*og*) and antheridium (*an*). B, same after separation of egg (*e*) from periplasm (*p*); *n*, egg nucleus; *an*, antheridium. C, section of oögonium, showing antheridial tube after its penetration of the egg. D, nearly mature zygote inside old oögonium, the antheridial tube, *at*, still extending into the thick wall. (C, from Wager, according to Mottier.)

within the host. The former is at first a globular cell with dense cytoplasm and many nuclei. Near it grows the antheridium, an irregular, club-shaped cell, containing several nuclei (Fig. 145, A). Within the oögonium all the nuclei but one, which remains in the center, pass into a zone along the periphery of the cell. Within this zone of nuclei a plasma membrane is formed delimiting a large, globular egg with its nucleus (Fig. 145, B). The cytoplasm and nuclei between the egg and the wall of the oögonium is the *periplasm.*

As the egg is being differentiated, the antheridium sends a tube into the oögonium, through the periplasm into the egg. The end of the tube opens, and one nucleus of the antheridium enters and fuses with the nucleus of the egg. This constitutes fecundation (C). The zygote develops its thick wall and passes into a dormant state. The thick wall, or at least a part of it, is doubtless formed at the expense of the periplasm.

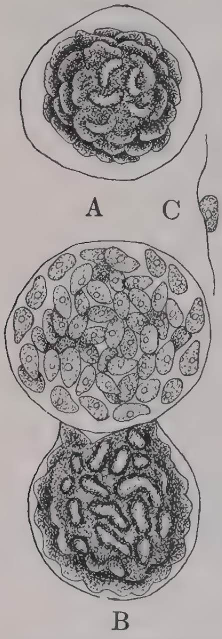

Fig. 146.—*Albugo candida.* A, surface view of mature zygote still enclosed in wall of oögonium. B, swarm spores escaping from germinating zygote. C, one swarm spore. (B, C, from DeBary.)

In some species, as in *Albugo bliti,* the egg contains several nuclei, and multiple fecundation results.

Germination of the Zygote and Infection of the Seedling Host.—In our climate the zygote passes the winter on the ground within the dead stems of the host plant. In the spring when the seeds of Capsella germinate the zygotes also germinate. The germination of the zygote results in the formation of many swarm spores (Fig. 146, B). If the swarm spores happen to come in contact with any part of the seedling host, infection will take place, and the seedling will grow up with its parasite.

How Albugo Secures Food from Its Host.—As shown in Fig. 147, the hyphae send into the cells of the host numerous very minute branches, *haustoria,* or suckers, the ends of which enlarge as soon as the cell wall is penetrated, so that each appears as a minute globular body connected with the hypha by a slender neck.

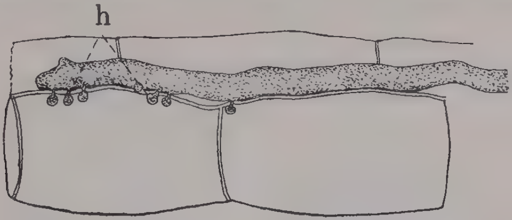

Fig. 147.—*Albugo candida.* Hypha between pith cells of the host plant. *h*, haustoria. (From DeBary.)

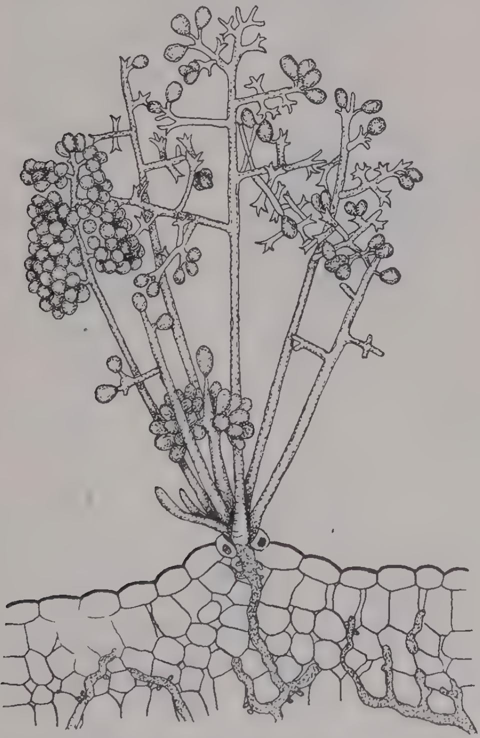

Fig. 148.—Section of leaf with much-branched conidiophores of *Plasmopora viticola* emerging through a stoma. (Adapted from Millardet's figure in Naturlichen Pflanzenfamilien.)

Other Destructive White Rusts.—Among other parasites resembling Albugo in character and life history are the downy mildew of the grape (*Plasmopora viticola*), the late blight of the potato (*Phytophthora infestans* DeBary) and the damping-off fungus (*Pythium debaryanum*), the last being often very destructive to seedling plants. The conidia of Plasmopora and Phytophthora are not found beneath the epidermis of the host as in Albugo, but on the outside. The conidiophores, which may be branched, grow out through the stomata or break through the epidermis (Fig. 148).

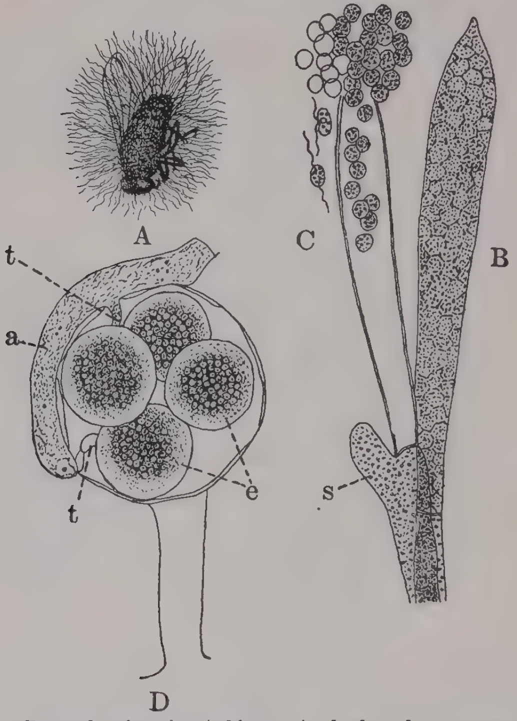

Fig. 149.—Reproduction in Achlya. A, body of a common fly with radiating filaments of the mould. B, sporangium with swarm spores nearly mature. C, sporangium discharging swarm spores; *s*, young sporangium. D, oögonium with antheridium (*a*) closely applied, and antheridial tubes (*t*) penetrating to the eggs (*e*). (B and C, from Engler & Prantl; D, from Trow.)

Water Moulds.—The mycelium of the water moulds is similar in structure to that of Albugo. These fungi may live as parasites or as saprophytes. They develop on the bodies of fishes and batrachians, and their eggs, or on the bodies of insects and other small animals that have fallen into the water. Their nature and reproduction are illustrated in Fig. 149.

The Fly Mould.—Species of the genus Empusa attack living insects. *Empusa muscae* is a parasite of the common house fly. The diseased flies are sometimes found in the autumn adhering to window panes and surrounded by a whitish halo of conidia, which have been shot off from the conidiophores protruding from the insect's body. The life history of this fungus is similar to that of the water moulds.

Classification of the Phycomycetes

The Phycomycetes may be included in the following orders:

1. *Chytridiales.*—These are among the simplest of the group, some consisting of a single small cell. Many are parasites on other fungi or on algae. Some species of Synchytrium are parasitic on seed-bearing plants.

2. *Saprolegniales.*—This order includes the water moulds, Saprolegnia, Acklya, etc., and the damping-off fungi.

3. *Peronosporales.*—This large group includes Albugo, Plasmopora, Peronospora, and Phytophthora.

4. *Mucorales.*—These are the bread moulds or pin moulds of the genera Rhizopus, Mucor, etc.

5. *Entomophthorales.*—Members of this order are parasitic upon insects, as species of Entomophthora mentioned in the foregoing.

MYCOMYCETES (EUMYCETES)—TRUE FUNGI

The vast majority of fungi belong to the Mycomycetes, or true fungi. Their mycelium, as a rule, consists of septate hyphae. With few exceptions they may be grouped into two great subdivisions, namely, the Ascomycetes (sac-fungi) and the Basidiomycetes (basidia fungi), which include smuts, rusts, mushrooms, and puffballs.

A typical sac, or ascus, is an elongated cell bearing commonly eight spores, although the number of spores in the ascus may vary (Fig. 161). A typical basidium is an elongated, or club-shaped cell bearing from one to four spores on very short and slender stalks at the upper end of the cell (Fig. 184, E).

ASCOMYCETES

Cultivated or Common Yeast (*Saccharomyces cerevisiae*).—In the classification of the fungi yeasts are sometimes included in the Ascomycetes, being placed in the sub-class Hemiascineae, because of the fact that when spores are formed the cell resembles a sac or ascus common to the Ascomycetes.

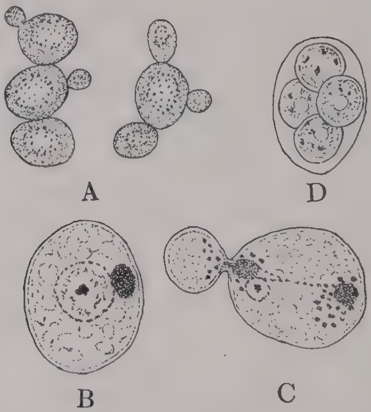

Fig. 150.—Yeast (*Saccharomyces cerevisieae*). A, actively growing cells showing budding. B, stained cell showing nucleus, cytoplasm, vacuole, and one conspicuous granule in vacuole. C, stained cell showing budding, the nucleus of the parent cell having divided. D, cell containing four spores. (A, D, from Campell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers. B, C, from Wager; D, from Riess.)

The yeast plant is unicellular, the cells often adhering to form a chain-like colony of cells. Rarely do the colonies become sufficiently long to be considered hyphae (Fig. 150, A, B). The cell contains one nucleus, and usually a large central vacuole and food granules.

Vegetative Propagation.—The cells multiply by a process of cell division termed "budding." A small bead-like protuberance is sent out at the end or side of the cell. The nucleus divides, and one of the daughter nuclei passes into the bud (Fig. 150, C). As the bud increases in size it is cut off by the completion of division. The new cell may soon divide in the same manner, and at the same time the parent cell may produce one or more buds at the sides or at the other end. If the new cells thus formed remain attached, a colony results.

Spore Formation.—Under certain conditions, as when the cells are cultivated on a piece of carrot or potato, internal cell division takes place, and two to four spores are produced (D). In this condition the yeast cell resembles a simple ascus.

Alcoholic Fermentation.—Yeasts are important in the economy of man chiefly because of certain useful by-products resulting from their life activity. The more important of these products are alcohol and carbon dioxide. When yeast uses glucose as a food, these two compounds result according to the following chemical expression: $C_6H_{12}O_6 = 2C_2H_5OH + 2CO_2$

Glucose, acted upon by zymase yields ethyl alcohol and carbon dioxide. In bread making the carbon dioxide liberated in the fermenting dough makes it rise.

The different species of yeast behave differently in regard to the fermenting substance, and this is an important matter in their use and classification. Some kinds of yeast consist of very small cells resembling bacteria, but they are distinguished from bacteria by the fact that yeast cells divide by budding, while bacteria divide by fission. A fungal spore, which closely resembles a bacterium or a yeast cell, is distinguished from these two by sending out a germ tube in germinating.

The Powdery Mildew.—Any common mildew, such as Sphaerotheca on the dandelion, Uncinula on the willow or Microsphaera on the lilac, will serve to illustrate the life history of one of the simpler Ascomycetes.

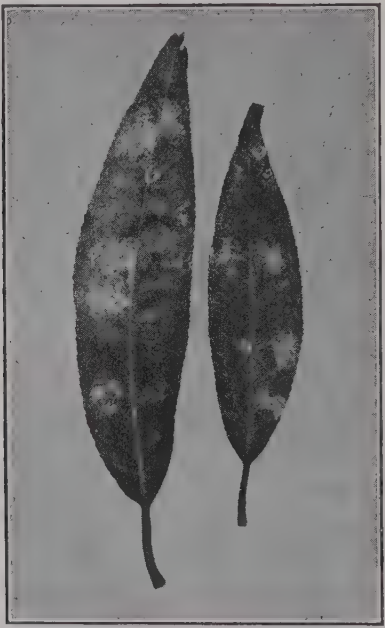

Fig. 151.—*Uncinula salicis.* Leaves of black willow, showing whitish patches of mycelium of the mildew, in which the small black perithecia can be seen.

These mildews are external parasites. Their mycelium, which consists of separate hyphae, forms a whitish or cobwebby weft on the surface of leaves (Fig. 151). Nourishment is secured from the host by means of haustoria sent into the epidermal cells of the leaf (Fig. 152, *c*). In Phyllactinia special short hyphae penetrate through the stomata more deeply into the tissues, sending haustoria into the underlying parenchyma cells.

Asexual Reproduction.—Asexual reproduction is effected by means of *conidiospores*, or *conidia*. They are formed in single rows, abjointed from the ends of upright hyphae (conidiophores), which arise at right angles from the mycelium (Fig. 152, *b*). When conidia are numerous the mildew presents the appearance of frosty or powdery patches on the surface of the leaf. Because of this fact they are called "powdery mildews." The conidia are borne chiefly by the wind to new host plants, where they germinate and give rise to new mycelia.

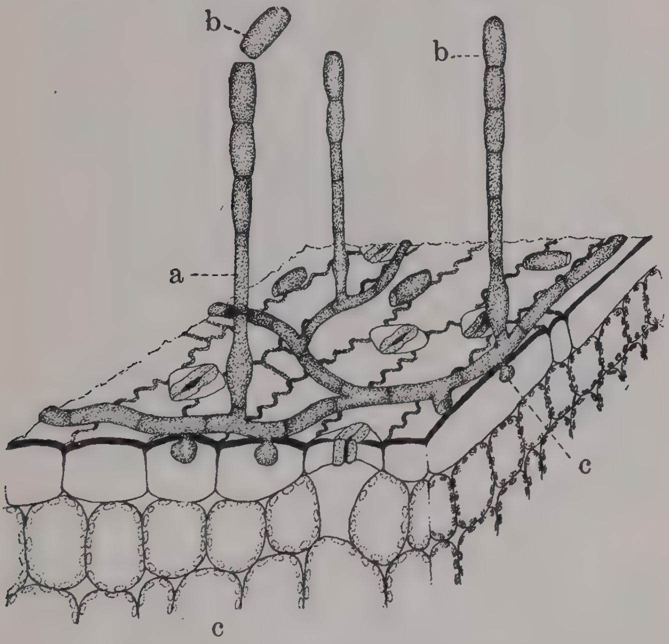

Fig. 152.—*Erysiphe graminis.* Formation of conidia in the mildew. Portion of a leaf of a grass, partly in section, showing mycelium, conidiophores (*a*), conidia (*b*), and haustoria (*c*). Leaf tissue diagrammatic.

Sexual Reproduction.—Later in the season the production of conidia ceases, and the mycelium develops the spore fruits (perithecia) as a result of sexual reproduction. The spore fruits are developed as follows: From adjacent hyphae two very short branches are sent up side by side, one being the oögonium and the other producing the antheridium (Fig. 153, A). The antheridium and its stalk are closely applied to the oögonium. An opening is formed between the two, and a nucleus from the antheridium enters the oögonium and fuses with its nucleus (B). After fecundation the vegetative cover

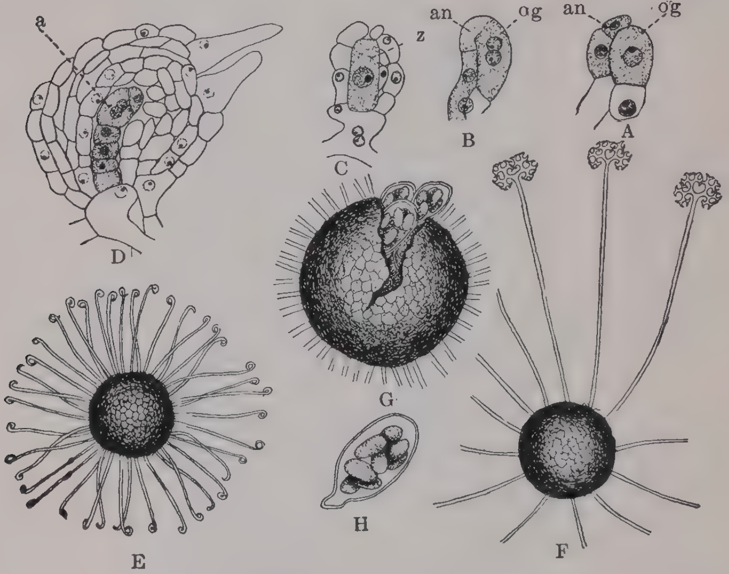

Fig. 153.—Sexual reproduction and formation of the perithecium in the mildew. A-D, first steps in the process in Sphaerotheca. A, antheridium (*an*) and oögonium (*og*) on portions of adjacent hyphae. B, union of oögonium and antheridium, with the gamete nuclei side by side. C, zygote (*z*) with the vegetative cover beginning to develop. D, row of cells (shaded) which have developed from the zygote. The large, binucleate cell (*a*) will give rise to the ascus or asci. The wall of the fruit is almost complete. E, mature perithecium of Uncinula. F, perithecium of Sphaerotheca. G, perithecium of Uncinula, broken open and showing the asci. H, one ascus of Uncinula. (A-D, from Harper.)

begins to grow up about the developing zygote enclosing it completely (C, D). This cover is derived chiefly from the hyphae that bore the sex organs. In the mean time the zygote produces a short row of cells. One of the cells near the end of this row, and which contains two nuclei that later fuse, develops into the single ascus in Sphaerotheca (D, *a*). The ascus contains eight ascospores. In Microsphaera and some other mildews two or more asci grow out of the binucleate cell. In some mildews the perithecia are without external appendages, but in others, as the spore-fruit matures, characteristic appendages are developed from the superficial cells of the perithecium (E, F).

The spore fruit with the contained ascospores serves to carry the mildew through the winter.

Diploid and Haploid Structures.—Those parts developing from the oögonium after fecundation, and producing the ascus or asci, constitute the diploid structure, inasmuch as the nuclei in those cells are descended from the zygote nucleus. The haploid structure is represented by the mycelium that bears the sex organs, and all subsequent parts of this mycelium resulting from purely vegetative growth. The shell or covering of the perithecium is, therefore, a part of the haploid structure.

Blue and Black Moulds.—Among simpler Ascomycetes that live saprophytically, as well as parasitically, are the genera Penicillium and Aspergillus. When mature the densely massed conidiospores appear blue-green or black, hence the source of their common names.

In sexual reproduction spore fruits are developed much in the same manner as in the powdery mildews, although the perithecia in some genera are much more complex than those of the mildews.

Asexual reproduction is accomplished by conidia, and the genera are usually recognized by the character of the conidiophores. In Penicillium the erect conidiophore produces whorls of branches, each branch bearing a chain of spores, the whole resembling a kind of brush or broom (Fig. 154, A). The conidiophore of Aspergillus is enlarged into a globular swelling at its upper end, from which grow out radially numerous short branches, each producing a chain of conidia (Fig. 154, B). In the genus Sterigmatocystis each branch from the globular enlargement bears two rows of conidia.

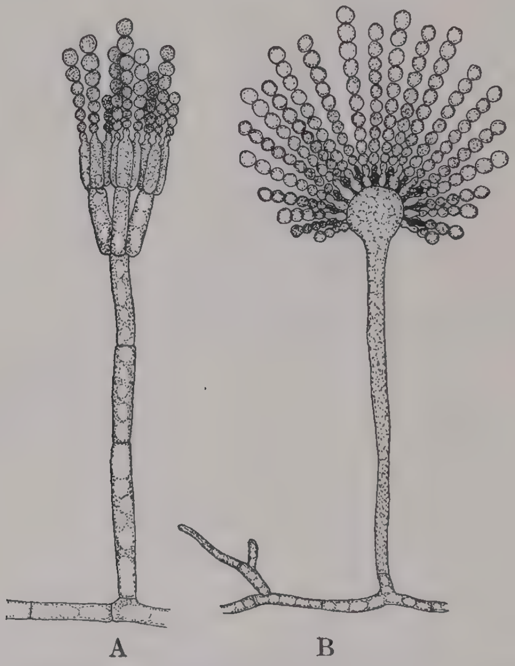

Fig. 154.—Conidiophores of blue and black moulds. A, Penicillium. B, Aspergillus. (From Kny's chart.)

Black Knot and Ergot.—Two very well known parasitic Ascomycetes are the Black Knot (Plowrightia) of the plum and other fruit trees, and the Ergot (*Claviceps purpurea*) on rye and other grasses. Plowrightia attacks the twigs of the plum tree inducing the large, rough malformations known as Black Knot (Fig. 155). Claviceps produces the large, purplish or black, horny ergot grains, which appear instead of normal seeds in the head of rye and other grasses (Fig. 156).

The mycelium of the ergot is recognized in the tissues of the flowers of the rye plant. The fungus develops rapidly, and soon destroys the ovary, replacing the normal kernel with the large mass of fungal filaments. This mass constitutes a "grain of ergot," and it is termed botanically a *sclerotium*, meaning a hard, dry, horny mass of fungal tissue.

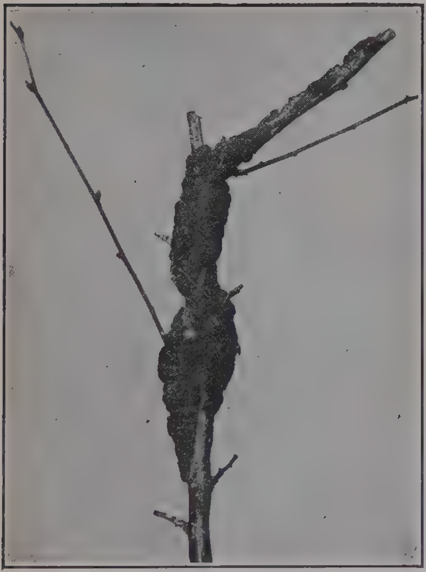

Fig. 155.—Twig of plum tree infected with the Black Knot fungus, Plowrightia. The black abnormal growth is the hypertrophied host tissue, in which are contained the mycelium and spores of the fungus.

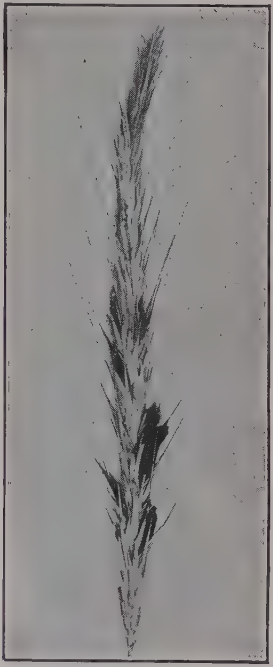

Fig. 156.—Head of rye with mature sclerotia of ergot.

The sclerotium drops to the ground, where it passes the winter. The following spring it resumes growth and sends out from one to several cylindrical or cord-like masses of fungal tissue, pinkish or purplish in color, and composed of bundles of numerous hyphae united laterally

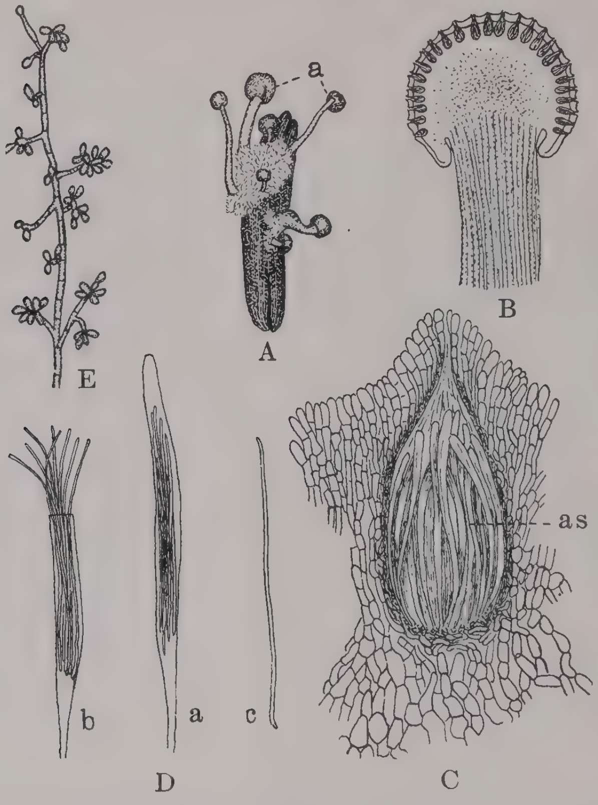

FIG. 157.—Ergot (*Claviceps purpurea*). A, sclerotium which has developed the bundles of hyphae ending in the rose-colored heads (*a*). B, longitudinal section of a head, showing location of apothecia. C, one apothecium enlarged; *as*, asci. D, ascus containing spores (*a*); with spores escaping (*b*); a single spore (*c*). (A-C, from Tulasne; D, from Brefeld.)

to form a pseudo-parenchyma (Fig. 157, A, *a*). Each cylindrical cord or mass bears at its free end a rose-colored head, in which numerous flask-shaped cavities, *apothecia*, are borne (B, C). The apothecia contain many slender asci, each with eight filiform ascospores

(D). These ascospores when set free are borne to the young flowers of rye where infection takes place.

Development of Conidia.—Upon the diseased flower and before the sclerotium is developed, the mycelium produces conidia (Fig. 157, E). At the same time a sweetish fluid, known as "honey dew," is exuded. This is sought by insects and, with the spores imbedded in it, borne to other host plants.*

Cordyceps.—Certain species of Cordyceps, which are related to ergot, are parasitic upon the larvae of the May beetle (Fig. 158).

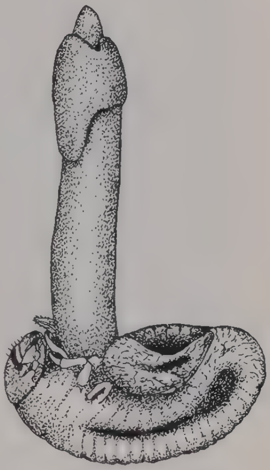

Fig. 158.—*Cordyceps herculea.* Spore-bearing structure growing from larva of the May Beetle.

Cup Fungi.—The cup- or disc-fungi, which are included in the class Discomycetes, are among the larger and more commonly known fleshy Ascomycetes. They grow generally on decaying wood or in humus. The spore fruit, known here as an *apothecium*, is in the form of a fleshy cup or flattened disc, varying in color from white to a brilliant scarlet, and in size from that of a pin head or smaller, as in Ascobolus, to several centimeters, as in Peziza and Bulgaria, etc. (Fig. 159, 160).

Peziza, Bulgaria.—As mentioned above, the spore fruit, or apothecium, of Peziza is in the form of a cup or flat, circular disk. The vegetative mycelium, which lives in the substratum, consists of a weft of hyphae or cord-like mycelial strands. The fruit is produced on the surface of the substratum. The inner surface of the cup, or upper surface of the disk, consists of a layer of club-shaped asci interspersed with numerous slender hyphae, often rich in oil, which are called *paraphyses*. The layer of asci and paraphyses constitute the *hymenium*. One of the functions of the paraphyses is to supply food material for the developing asci (Fig. 161).

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* From ergot is prepared for officinal use, under legal regulations, a powerful drug. The sclerotium is poisonous to stock if eaten in sufficient quantity, causing a malady which leads to the loss of hoofs, horns, and tail.

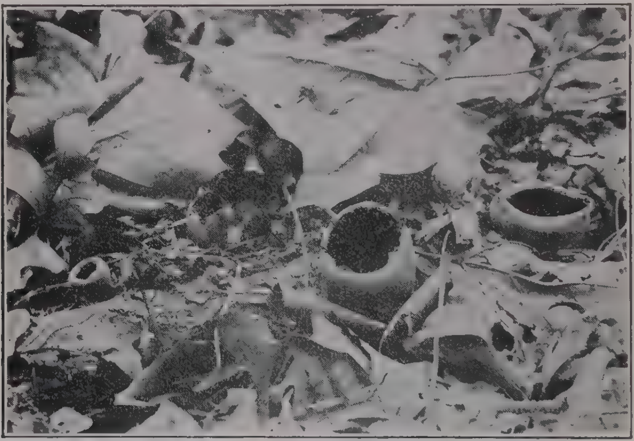

Fig. 159.—*Urnula craterium*. Apothecia in natural habitat on dead branch of elm.

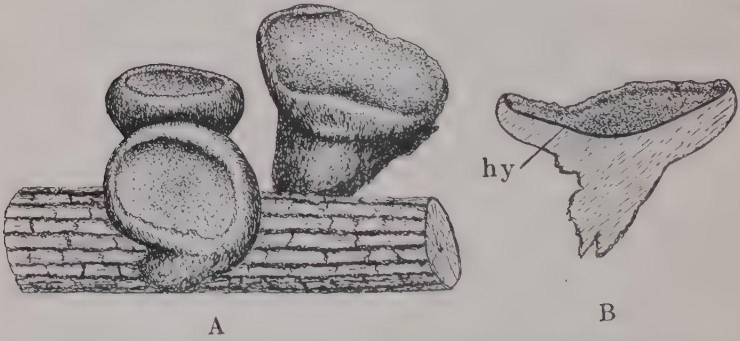

Fig. 160.—*Bulgaria inquinans*. A, apothecia in different stages of development, on dead branch of oak. B, vertical section of an apothecium; *hy*, hymenium.

Sexual Reproduction, and the Formation of the Apothecium.—As in many other Ascomycetes, the spore fruit consists of a reproductive part surrounded by a vegetative cover. Its development has been followed in greatest detail in *Pyronema confluens*, a fungus whose yellowish or reddish apothecium is about one millimeter in diameter.

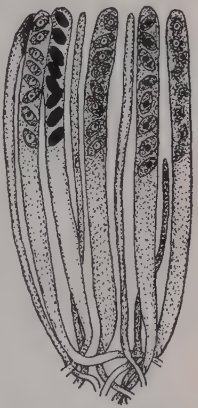

FIG. 161.—*Bulgaria inquinans*. Vertical section of a part of the hymenium, showing asci and paraphyses.

Several oögonia and antheridia take part in the formation of the apothecium. They arise on a weft of the mycelium side by side in a cluster (Fig. 162, A). The oögonium (*o*) is a large, globular cell, from the top of which grows out a generally curved tubular cell, the trichogyne (*t*), which finally fuses with the upper end of the club-shaped antheridium (*a*). The oögonium, antheridium, and trichogyne are multinucleate. The egg does not round up and separate from the wall of the oögonium. Its behavior in this respect resembles that of the Red Algae. The nuclei in the trichogyne disorganize; the wall between the oögonium and the trichogyne is dissolved, and some of the contents of the antheridium passes through the trichogyne into the oögonium, where the male and female nuclei fuse in pairs (B, C, D).

From the surface of the oögonium will now grow out numerous branched *ascogonous* filaments (E, *af*). From the ends of these the asci will ultimately be formed as the result of a complex process of nuclear and cell division. During the development of the ascogynous hyphae there grow up among them many vegetative hyphae, which produce the paraphyses. At the same time the vegetative part of the plant increases and grows up about the asci and paraphyses, completely enclosing them. It will thus be seen that in the immature apothecium the hymenium is enclosed. As it matures, however, an opening forms in the top, and the hymenium is exposed. The apothecium may remain a deep cup, or growth may continue in such a way as to open out the cup into a flat disk.

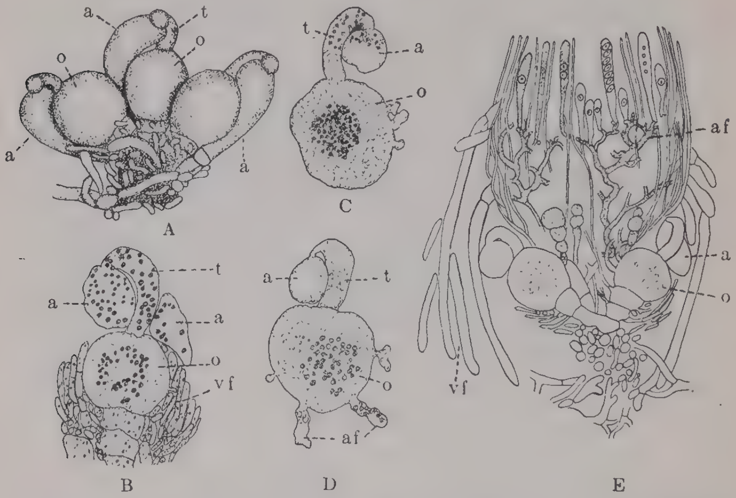

Fig. 162.—*Pyronema confluens.* Fecundation and early stages in the formation of the apothecium. A, cluster of oögonia (*o*), with trichogyne (*t*) and antheridia (*a*). B, fusion of antheridium with tip of trichogyne; *vf*, vegetative filaments. C, fusion of male and female nuclei in pairs after dissolution of basal wall of the trichogyne. D, oögonium cut off from trichogyne by a new wall, and ascogenous filaments (*af*) beginning to grow out from the oögonium. E, vertical section through a very young apothecium; ascogenous filaments (*af*) bearing asci. (From Harper.)

From the foregoing we see that the development of the apothecium in the Discomycetes is similar to that of the perithecium in the mildews.

Morchella Esculenta.—The morel, which is often highly prized as a delicacy of the table, is one of the largest and most highly differentiated of the Discomycetes. (Fig. 163). The irregular depressions in the crinkly head of the morel are lined with a hymenium bearing many asci. This part of the plant is regarded by some as a sort of compound apothecium. The morphological history of the morel is unknown. The vegetative mycelium lives in the soil.

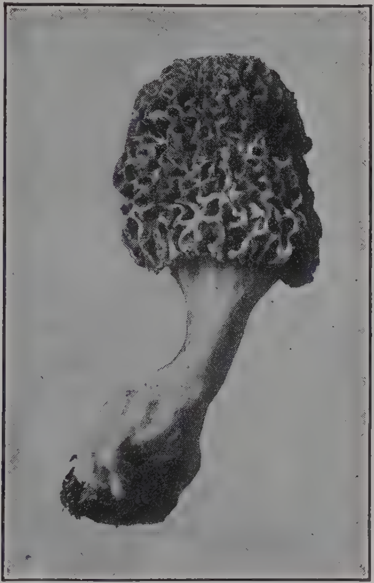

FIG. 163.—The mature sporophore of *Morchella esculenta*.

The Truffle.—The truffle of commerce is the large spore fruit of certain species of the genus Tuber. These develop underground, where the mycelium lives saprophytically. The edible truffles are obtained chiefly from France and Italy. The species found in Indiana have small spore fruits which are said to be poisonous.

Lichens.—With very few exceptions every lichen consists of two different plants, an alga and a fungus, living together in such a way as to constitute a single individual. The fungal part completely surrounds the algal constituent (Fig. 164, C). In a sense, a lichen is a fungus with an alga imprisoned in its mycelium. Since the fungus concerned is usually an Ascomycete, lichens are sometimes regarded as members of the Ascomycetes

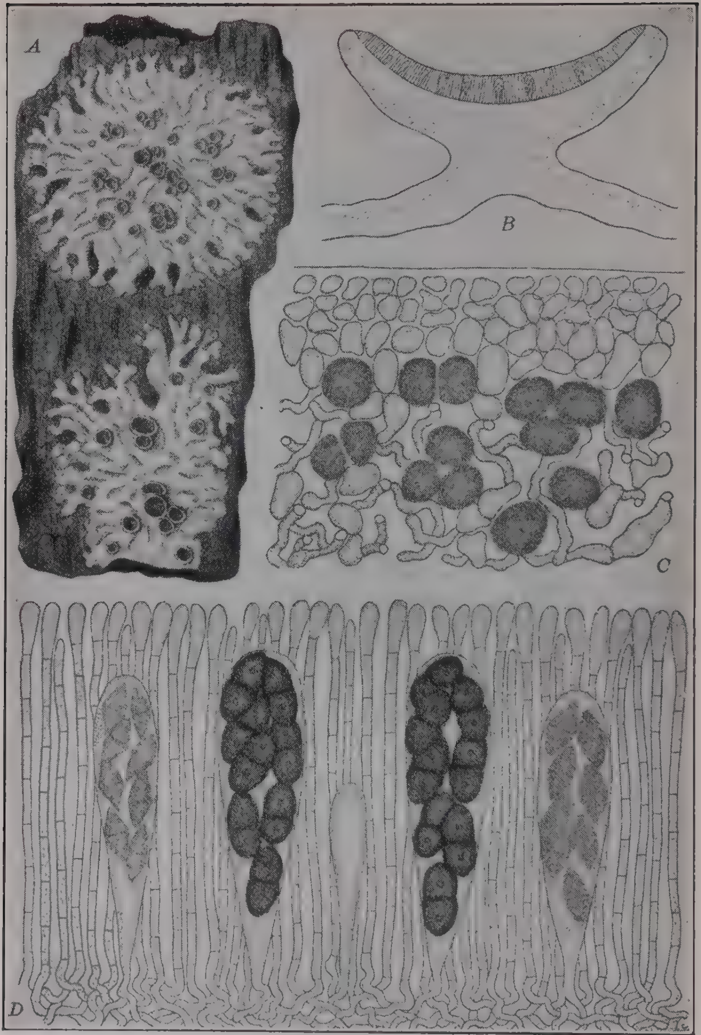

Fig. 164.—A common Tree Lichen (*Physcia stellaris*). A, habit sketch; B, diagram of a vertical section through a spore-fruit (*apothecium*), showing the hymenium, and the position of the algal cells (Protococcus) among the fungal filaments; D, section of the hymenium, with asci in different stages of development and the slender paraphyses. (From Bergen and Davis' "Principles of Botany." By permission of Ginn & Company, Publishers.)

which imprison algae in their thalli. In a small group of tropical lichens (*Cora pavonia* and other species) the fungal constituent is a Basidiomycete. The alga is usually some species of the Cyanophyceae or of the Protococcales.

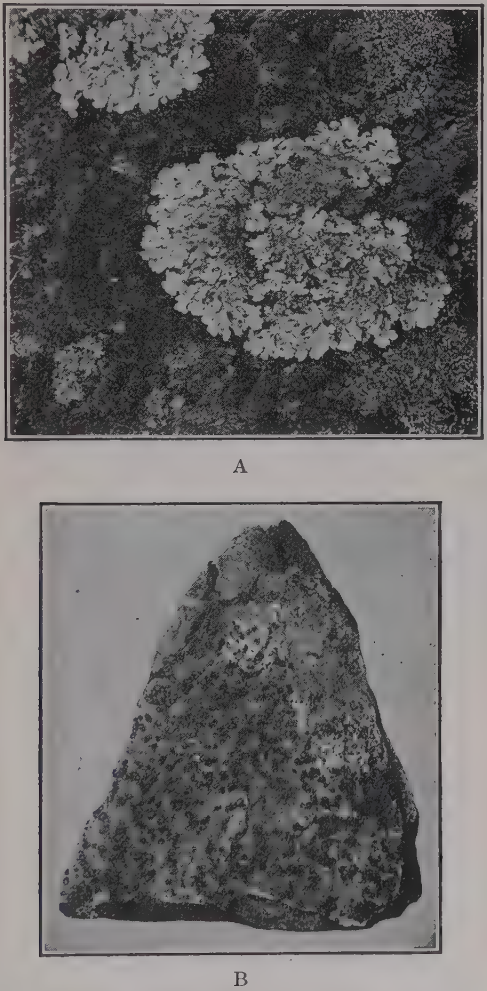

Fig. 165.—A, foliose Lichen, Parmelia; B, crustose Lichen.

The green or bluish-green color of a lichen is usually dull in appearance because of the translucent fungal or gelatinous covering over the algal constituent. Many lichens have additional pigments such as yellow, orange, reddish, or brownish.

Based upon the form of the plant body, three classes of lichens are recognized: (1) *Crustose* lichens, with poorly defined mycelium, which frequently penetrates the substratum and forms incrustations on rocks, etc. (Fig. 165, B); (2) *Foliose* lichens, flat and leaf-like, with lobed or irregular margins (Parmelia, Physcia, Figs. 164, 165, A); and (3) *Fruticose* lichens, gelatinous (Collema), bushy and erect (Cladonia, Fig. 166), or pendent (Usnea, Fig. 167). Some, however, are filamentous.

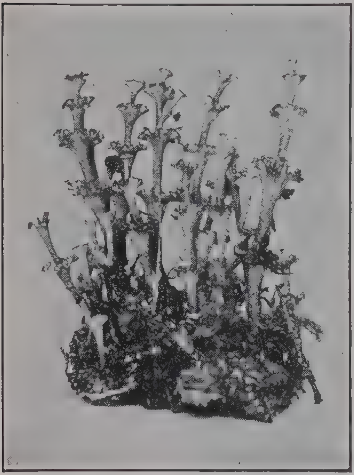

FIG. 166.—Cladonia, bushy and erect Lichen.

The Thallus.—In gelatinous lichens, such as Collema, in which the alga is a species of Nostoc, the filaments of both alga and fungus are irregularly distributed in a gelatinous matrix (Fig. 168, A).

The structure of the forms more commonly encountered may be illustrated by Parmelia or Physcia. The plant body of Parmelia is a flat, irregularly lobed, tough, leathery, grayish-green thallus. The lower side is generally whitish. The thallus is fastened to the substratum by numerous *rhizines*, which are strands of mycelium. The upper and lower portions of the thallus form a firm, tough cortex composed of interwoven fungal filaments. Inside the cortex, but nearer the upper surface is a region of looser fungal tissue among whose

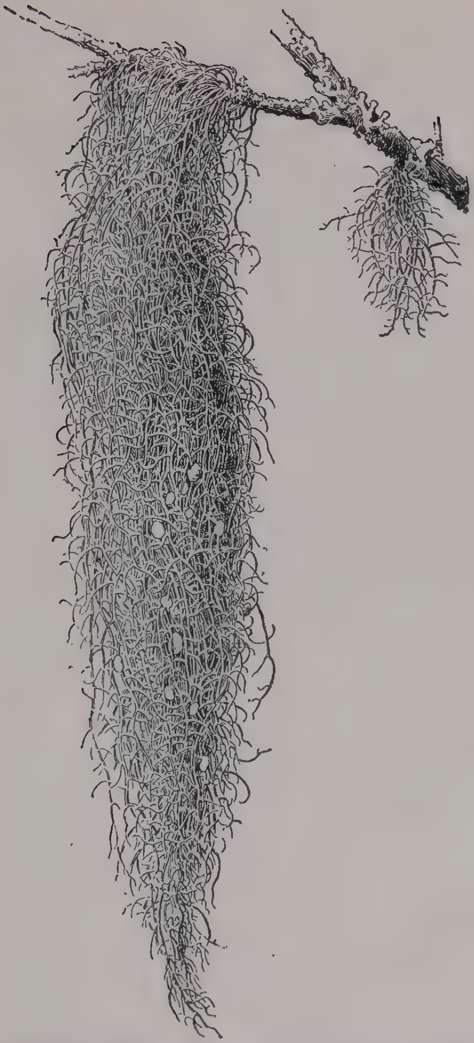

FIG. 167.—Fruticose Lichen, Usnea, hanging from a spruce twig which supports also Parmelia. The Usnea bears several disk-like apothecia. (Adapted from Caldwell's "Practical Botany." By permission of Ginn & Company, Publishers.)

filaments are embedded in a definite stratum the algal cells, here a species of Protococcus. The central part of the thallus consists of more loosely woven filaments forming a sort of pith (Fig. 164, C).

Relation of Alga and Fungus.—The alga found in the thallus of a lichen can and does live in the free state, entirely separate from any association with a fungus. It is generally conceded, however, that the fungus is parasitic upon the enclosed algal cells. Some of the latter are penetrated by haustoria of the fungus and injured or killed. In other cases it seems that the fungus obtains nourishment from the alga by mere contact. Many of the algal cells, apparently uninjured by the fungus, continue to grow and divide. On the whole the algal constituent does not seem to be greatly injured by the fungus, and it is highly probable that it receives some benefit in the protection provided and the more uniform conditions of moisture and temperature afforded.

The living together of two different species of organisms is known as *symbiosis*. The relation of alga and fungus in the lichen is nutritive, one of the symbionts at least, receiving nourishment from the other. When each symbiont contributes to the welfare of the other, we have *mutualistic* symbiosis. In the case of the Lichen under consideration, the status of the alga is that of enforced slavery. Such a relation is styled *helotism*, master and slave.

Vegetative Propagation.—Many lichens propagate vegetatively by the separation from the surface and edges of the thallus of minute proliferations known as *soredia*. These are often so numerous that they appear as a greenish or gray powder covering large areas of the surface of the thallus. Each soredium consists of a few algal cells held in a tangle of short pieces of hyphae. They are readily distributed by the wind and other agencies, and, if deposited in favorable locations, develop into new lichens.

Sexual Reproduction.—The production of ascospores in a lichen is accomplished exclusively by the fungus, the alga taking no direct part in the process. In Parmelia or Physcia the apothecia are small, cup-shaped or disc-shaped bodies slightly elevated above the surface. The bottom of the cup, or the surface of the disc, is lined by the *hymenium*, consisting of upright asci interspersed with slender *paraphyses* containing a reddish, oily food substance (Fig. 164, B, D). The wall of the apothecium is composed of the vegetative part of the thallus, consisting of algal and fungal layers. Each ascus contains eight spores, which become two-celled before being discharged.

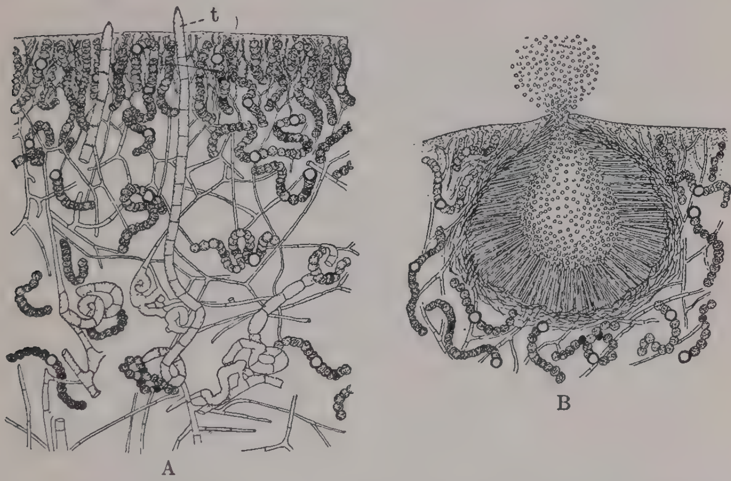

Fig. 168.—Sex organs of a gelatinous lichen, Collema. A, section of thallus, showing the oögonium; *t*, end cell of trichogyne. One of the cells of the coiled part is the egg. B, spermagonium. Sperms (spermatia) are formed from the ends of very slender hyphae. (A from, Kny's chart; after Stahl. B, adapted from Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers.)

Lichens are very difficult plants to study structurally, and the origin of the spore-producing part of the apothecium is known definitely in only a few species. It was discovered by Stahl, and later verified by Bauer and

Darbyshire, that the sporogenous filaments of the apothocium are developed as the result of a sexual process.

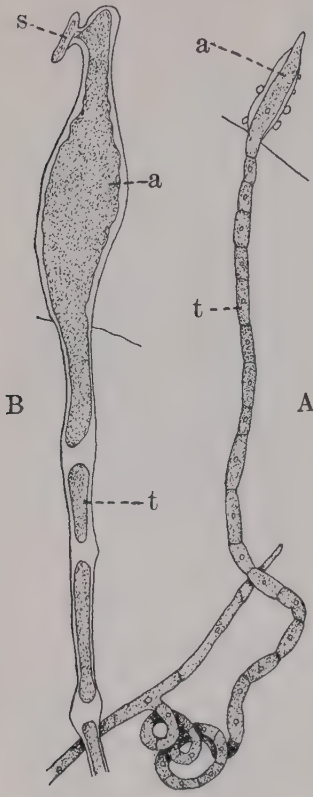

FIG. 169.—Oögonium (carpogonium) of Collema crispum. A, the long, multicellular trichogyne (*t*) ending above the surface of the thallus in a large receptive cell (*a*). The egg cell is one of the cells of the coiled portion. B, upper end of a trichogyne (*t*) with sperm (*s*) attached to receptive cell. (From Bauer.)

The oögonium is a long multicellular filament, coiled at the base and continued in a straight portion, the distal end of which projects slightly above the thallus (Fig. 168, A, *t*). One of the cells of the coiled part represents the egg; the straight part is the trichogyne.

The male gametes are formed in small conceptacles (spermagonia), which open at the surface by means of a small pore (Fig. 168, B). At the ends of slender upright hyphae in the spermagonia small unicellular *spermatia* are cut off. These are equivalent to the sperms of other plants. After being discharged from the spermagonia the spermatia are washed by water to the projecting part of the trichogyne, to which they adhere (Fig. 169, B, *s*). The sperm unites with the trichogyne, and its nucleus presumably passes from one cell to another, through small openings in the walls, down to the egg (Fig. 169, B). After fecundation numerous sporogenous filaments grow out from the coiled portion of the oögonium, and finally give rise to asci at their upper ends.

In the meantime numerous slender hyphae, the paraphyses, grow up among them from the vegetative mycelium near the region of the oögonium. The asci and the paraphyses form the hymenium of the apothecium. The wall of the apothecium is, as has been stated, a vegetative growth of the thallus. The apothecium develops as a closed structure, opening at maturity to form a cup or disc.

In *Collema pulposum*, according to Bachman, the sperms are not borne in spermagonia, but terminally and laterally on hyphae below the surface. They are, therefore, completely embedded in the thallus and never set free. The trichogyne, consequently, does not grow to the surface of the thallus as described in the foregoing. Its terminal cell, which becomes greatly elongated, grows horizontally towards the region where the sperms are borne, and the union of the sperm and the trichogyne takes place within the thallus. Water as an agency of the transfer of sperms to the trichogyne is doubtless eliminated in species like *Collema pulposum*.

It is evident, therefore, that the spore fruit of the lichen, as in many other Ascomycetes, represents a *spore-producing structure* developed as a result of gametic union, and a surrounding *vegetative part* that arises from the vegetative thallus. In its development, therefore, the lichen apothecium parallels that in Peziza, Bulgaria, Pyronema, and certain other Ascomycetes.

Geographic Distribution.—Lichens occur widely distributed over the surface of the earth from the tropics to the arctic regions. They live on rocks, tree trunks, etc., and very often in places where conditions are too severe for other vegetation. They are very abundant in moist northern countries such as Alaska, northern Europe, and Siberia. There they constitute one of the more important forage plants for such animals as the reindeer. In the economy of nature also they play the role of rock disintegrators and soil formers. Some lichens are parasitic on the leaves of trees and on various parts of other plants.

Uses to Man.—For ages certain lichens have been used for food by various peoples. Iceland moss (*Cetraria islandica*) is ground up and mixed with wheat and made into cakes. *Lecanora esculenta* was eaten by people in southwestern Asia in ancient times. In eastern Siberia lichens prepared in various ways constitute an important part of the vegetable diet of certain classes of the inhabitants. Poisons, drugs, perfumery, and alcohol have been prepared from certain lichens. From *Roccella tinctoria*, found in the East Indies, on the coast of Africa, and possibly along the northern coast of North America, litmus and the dye, orchil, are derived. Other dyes of blue, purple, red, and crimson are also extracted from lichens.

BASIDIOMYCETES

In this subdivision of the fungi are included all those Mycomycetes in which certain spores are borne on special cells known as *basidia*. As used in this book a basidium will be understood to consist generally of an elongated cell from whose upper end are produced one or more spores, usually formed at the ends of very slender processes called *sterigmata*. Typical basidia are shown in Fig. 183 and in Fig. 184 E.

The lower basidiomycetes are represented by the smuts and rusts; the higher representatives include the large fleshy forms like the field mushroom, puff balls, and stink horns, as well as the woody shelf fungus and the like.

Ustilaginales, Smuts.—The smuts are internal parasites, the mycelium living mostly within the intercellular spaces of the host. They are well known and of great economic importance because of their injurious and destructive effect on the cereal crops and some other economic plants such as the onion. Although best known on members of the grass family, the smuts occur on species of many other families of plants widely

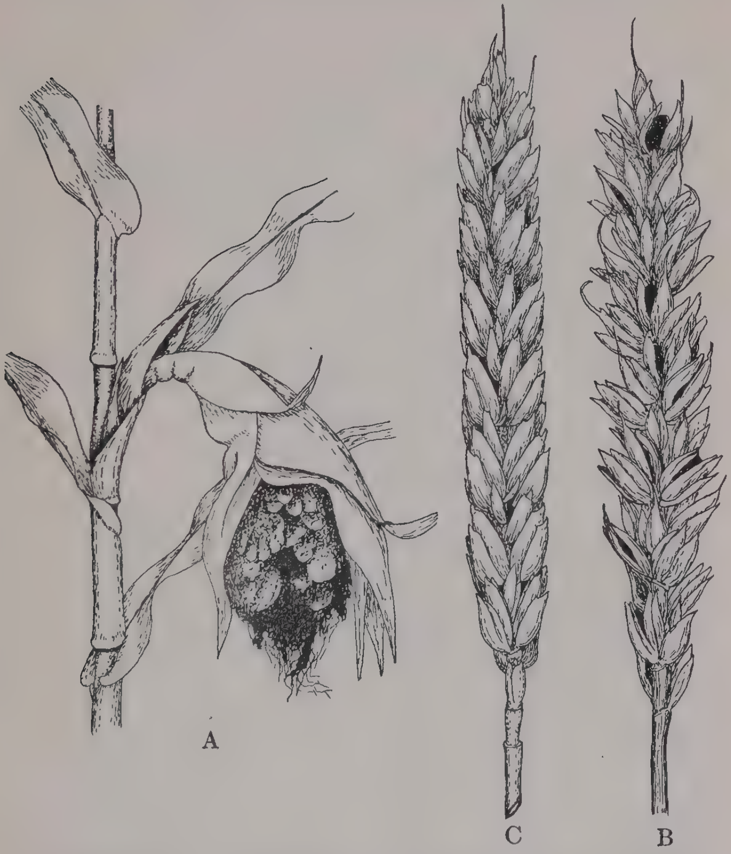

FIG. 170.—Habit of common smuts. A, Ustilago on corn. B, Tilletia on wheat. C, normal head of wheat.

separated in relationship. Most smuts are easily recognized by their black, sooty masses of spores produced in large quantities on various parts of the host plant, as on the stalk, blades, tassels, and ears of Indian corn, and in the heads of oats, wheat, sorghum, etc. (Fig. 170, A, B). Certain smuts develop the black spores in the anther of the flowers of the host in the place of pollen grains which are destroyed by the parasite.

Asexual Reproduction.—Two kinds of spores are primarily produced, the smut spores, *chlamydospores*, and the *basidiospores*. In some cases other spores, which will de designated as *secondary sporidia*, are also developed. The sooty masses seen on the host are composed of countless numbers of very small chlamydospores. This spore has a rather thick and firm, dark brown or black wall, which may have various external markings, such as spines or ridges. In some species this spore has one nucleus; in others it may have two. These spores are formed from undifferentiated hyphae of the mycelium, the short cells of which enlarge, round out, and develop the thick cell wall (Fig. 171, A, B). The spores are scattered by the wind or adhere to the kernels of the threshed grain.

Germination of the Chlamydospore.—In most smuts when the chlamydospore germinates it produces a short hypha usually four cells in length. Each cell produces at its upper end one or more small spores (Fig. 171, C, D). The similarity between this hypha and a typical basidium is the basis for including the smuts in the Basidiomycetes. The whole hypha is regarded as a modified basidium, and the spores that it produces are probably the equivalent of the basidiospores of other Basidiomycetes.* In general a basidium consists of one cell as stated in the foregoing.

There is, however, much variation in the behavior of the hypha produced by the chlamydospore. Under experimental conditions two or more basidia may be produced from one chlamydospore. In *Tilletia tritici* only the distal cell of the basidium produces spores (Fig. 171, E). These frequently fuse in pairs, and the paired spores germinate forming sickle-shaped secondary spores (Fig. 171, F). This fusion of spores was formerly supposed to be a sexual fusion, but it is not usually so regarded at present.

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* In the older literature, when this relationship was not evident, the short hypha produced from the chlamydospore was spoken of as the *promycelium*, and its spores as *sporidia*.

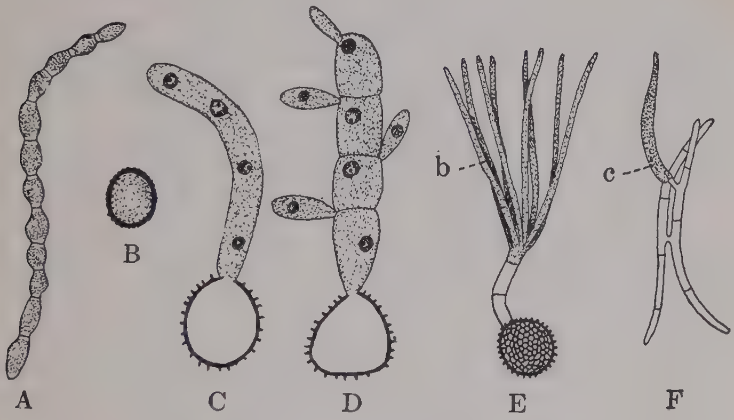

Fig. 171.—The chlamydospore of smut, and its germination. A, a piece of hypha forming chlamydospores. B, a single spore. C, D, germination of chlamydospore of *Ustilago scabosiae;* C, the hypha containing four nuclei; D, the hypha divided into four cells, each bearing a basidiospore. E, F, *Tilletia Tritici*, the stinking smut of wheat; E, basidium produced from a chlamydospore, bearing four pairs of spores, *b*; F, germination of a pair of basidiospores, producing a sickle-shaped sporidium, *c*. (A, E, F after Brefeld; C, D after Harper.

On germination the basidiospore or the secondary spore produces an infection tube which enters the seedling as it leaves the seed coat. In the loose smut of wheat no basidiospore is produced, the chlamydospore giving rise directly to the infection tube.

Does Sexual Reproduction Occur in the Smuts?—When grown in culture media under experimental conditions the basidiospores undergo division by budding, producing chains or colonies of cells resembling yeast plants. These frequently unite by a conjugating tube, but there is no fusion of nuclei. Sometimes the adjacent cells of the basidium also unite by a conjugating tube. Until nuclear fusions can be demonstrated in such cases these unions will probably be regarded as merely vegetative fusions having only a nutritive function.

Economic Importance.—Smuts do great injury to the cereals and other crops, and various methods are used in efforts to minimize the damage done. In the case of the oat smut and the stinking smut of wheat the seed grain is treated with formalin to kill adhering smut spores. For the loose smut of wheat, in which the mycelium is already in the grain, infection having taken place in the flower, the hot water treatment has been used with success.

Selection of seed, and the development of resistant varieties through plant breeding are other means of attack.

In corn smut treatment of the seed is useless because the spores responsible for infection pass the winter in the soil.

UREDINALES—RUSTS

The rust fungi have received their common names from their appearance at certain times, when their bright orange or red spores resemble iron rust. These fungi are of great economic importance because of their destructive effects upon their hosts, many of which are plants useful to man. They are also of unusual botanical interest because of their complicated life histories and the problems which the life histories present.

In the complete life history of some species as many as four kinds of functional spores may be produced, and more than one host may be involved. The different stages of the same species,—growing on different hosts, or in different seasons,—resemble one another so little in some cases that they have been regarded in the past as different species of fungi. In other species fewer than four kinds of spores may be produced, and often only one host is required.

The Grain Rust (*Puccinia graminis*).—As a concrete illustration of a rust fungus with a long and complicated life history, the classic *Puccinia graminis* is selected. This fungus is variously known in different localities as Wheat Rust, Red Rust, Black Stem Rust, or Grain Rust. Its two host plants are the tall barberry (*Berberis vulgaris*) and some species of grass, such as wheat, rye, oats, etc. Four distinct phases of the parasite's life history may be recognized.

Uredinial* Stage on the Wheat.—The presence of the uredinial phase of the rust on this cereal may be recognized by the development of numerous orange-colored pustules upon the blade or sheath of the leaves (Fig. 172, A). Each of these is a *uredinium*, which has been formed beneath the epidermis, from the mycelium growing in the intercellular spaces of the host, and which contains numerous *urediniospores*.

The *urediniospores* are developed singly at the ends of upright hyphae. Each spore has two nuclei, and a thick cell wall variously marked externally and provided with thin places known as *germ pores* (Fig. 173, A, *u*). There are two or more germ pores in the region of the equator of the spore. The color is due to reserve food in the form of a reddish oily substance. Urediniospores blown to other host plants infect them immediately, and a new crop of the same kind of spores may be produced in a few days. In this way a large acreage may be infected in a week or ten days of favorable weather.

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* Throughout this discussion the terminology used will be that of the modern literature on the rusts. Some of these terms, with their equivalents in the older literature, are as follows: uredinium = uredosorus; urediniospore = uredospore; telium = teleutosorus; teliospore = teleutospore; basidiospore = sporidium, spring spore; aecium = aecidium; aeciospore = aecidiospore; pycnium = pycnidium spermagonium; pycniospore = spermatium.

Telial Stage.—Later in the season, often as the host plant is approaching maturity, the uredinial phase of the rust gradually changes into the telial phase. The latter is characterized by dark brown or black pustules (*telia*) on various parts of the host, especially the leaf sheaths and the stem (Fig. 173, B). In this phase the rust is most destructive when it occurs on wheat. This is the dreaded Black Stem Rust. The telia contain thick-walled, two-celled *teliospores*. Each cell of this spore has a single nucleus. At the time of the transition from the uredinial to the telial phase both urediniospores and teliospores may be found in the same sorus (Fig. 173, A).

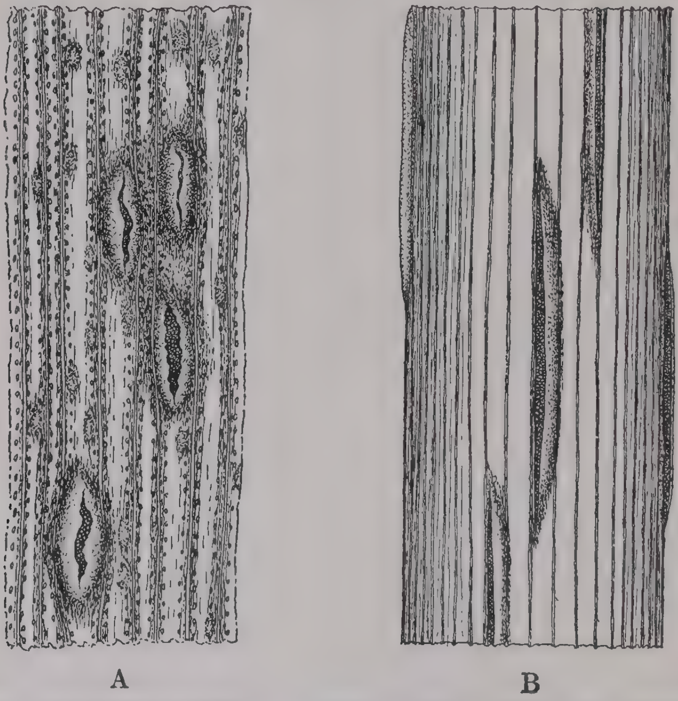

Fig. 172.—*Puccinia graminis*. A, portion of leaf of wheat with uredinia, B, portion of stem of wheat with telia.

Basidial Stage.—The teliospore is a resistant structure, remaining dormant during the winter in the old straw, or on the ground. On germination in the following spring each of its cells puts out a short hypha four or five cells in length (Fig. 173, C). Each cell of this hypha produces a small spore on a slender stalk. Formerly this hypha was known as a promycelium, and its spores as sporidia, or spring spores. Because of the similarity between the promycelium and certain structures to be discussed later, it is now generally regarded

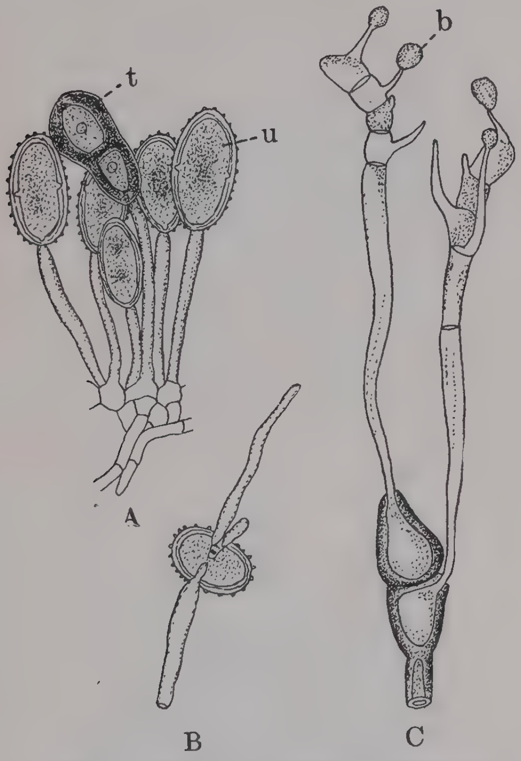

Fig. 173.—*Puccinia graminis.* A, portion of a uredinium, showing urediniospores (*u*) and one teliospore (*t*). B, germinating urediniospore. C, germinating teliospore, with basidiospores (*b*). (A and B, after DeBarry, C, after Tulasne.)

as a *basidium*. The spores which it produces are, accordingly, *basidiospores*, and the stalks on which the spores are borne are *sterigmata*. No host is required for the production of basidiospores.

Aecial Stage.—The basidiospores are scattered by the wind, and, in so far as is known as present, they can infect no plant but the tall barberry (*Berberis vulgaris*) or some of its near relatives. It is interesting to note, however, that the Japanese barberry (*B. Thunbergii*) so much used as an ornamental shrub, is immune. Infection of the barberry takes place in the early spring, and yellowish blotches soon appear on its leaves. On the lower side of the leaf in each of these blotches clusters of minute cups (*aecia*) will soon burst through the epidermis, and the corresponding upper surface will be marked by minute black dots, which are the openings of small cavities (*pycnia*) formed beneath the epidermis (Fig. 174, A, B).

The aecia are filled with orange-red *aeciospores*, which are blown away to the proper grass plant, in this case the wheat, to give rise to the uredinial phase again. The pycnia produce numerous small spore-like bodies, *pycniospores*.

Details of the aecial phase are best seen in vertical sections through a diseased spot of the leaf of the host, where hypertrophy occurs to such an extent that the leaf is two or three times its normal thickness.

The aecium has a definite wall of fungal tissue. It is formed beneath the epidermis, but at maturity the accumulation of spores ruptures the epidermis (Fig. 175, *a*, *b*). The wall of the cup is also ruptured at the top, and its edge curves outward. Chains of aeciospores are borne on erect hyphae arising from a weft of mycelium in the bottom of the cup. In each chain the spores alternate with small, flattened intercalary cells. The spores and the intercalary cells are binucleate, but the mycelium from which they are produced is made up of uninucleated cells.

The pycnia are small, flask shaped cavities whose walls are covered with erect hyphae from which the pycniospores are cut off (Fig. 175, *c*). They appear in advance of the aecia of the same diseased spot. For some years students of the rusts, as a rule, have looked upon the pycniospores as functionless male gametes, the pycnium representing an antheridium in the phylogenetic history of the fungus, and now functionless.

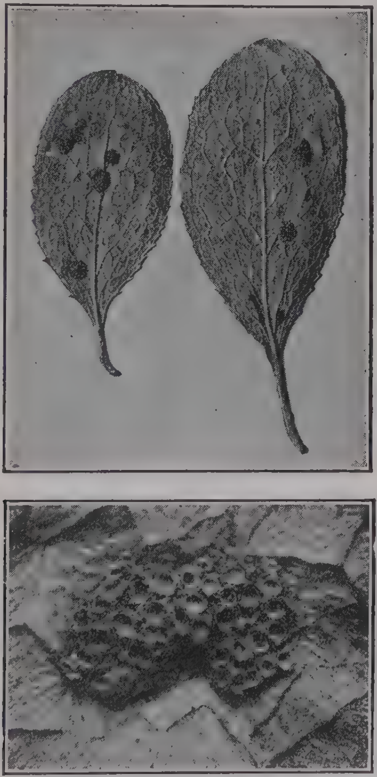

FIG. 174.—*Puccinia graminis.* Leaves of barberry, showing clusters of aecia.

It has been claimed recently that if the pycniospores produced upon one diseased spot are transferred to another spot whose mycelium is presumably of a different sex, they will germinate and the resulting mycelia will function with the mycelium of that spot in producing the diploid condition.

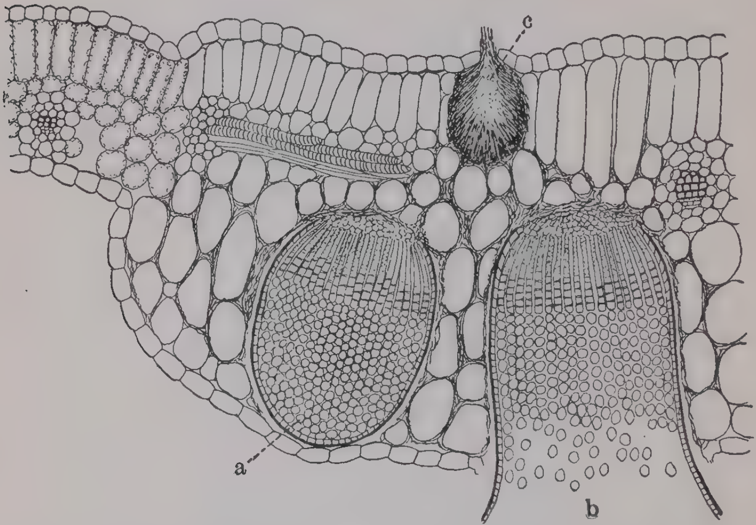

Fig. 175.—Cross section of portion of leaf of barberry including a portion of a spot infected with Puccinia. The extent of the hypertrophy may be seen in comparison with the normal condition of the leaf as shown at the left. *a*, an unopened aecium; *b*, an opened aecium; *c*, a pycnium. (Diagrammatic.)

Development of the Aeciospores.—*Indications of Sexuality.*—It will be noted that certain cells of this rust have been described as uninucleate (haploid) and others as binucleate (diploid). This occurrence is generally interpreted as a manifestation of sexuality. The details, which have been investigated in a few rusts, and are supposed to be of general occurrence, may well be described here as it occurs in a species of Phragmidium.

The mycelium of the aecial stage is made up of uninucleate cells. The aecium begins in a weft of hyphae formed beneath the epidermis. From this weft grow up side by side a number of club-shaped cells, each containing a nucleus (Fig. 176, A). Each club-shaped cell now divides into a small distal cell and a large basal cell (Fig. 176, B, *d*, *g*). The distal cells (*d*) disorganize and become crushed out. The basal cells elongate slightly and assume the general character of gametes, fusing in pairs. They elongate slightly and fuse at the upper ends (Fig. 176, C). The united ends continue growth as a single hypha (Fig. 176, D). The nuclei pass into the new portion and remain associated, side by side, but do not fuse. They now divide simultaneously, and a cell is cut off containing two of the daughter nuclei lying side by side, the other daughter nuclei remaining in the cell below (Fig. 176, D, E). The cell cut off (*s*) is the initial cell of the aeciospore. It

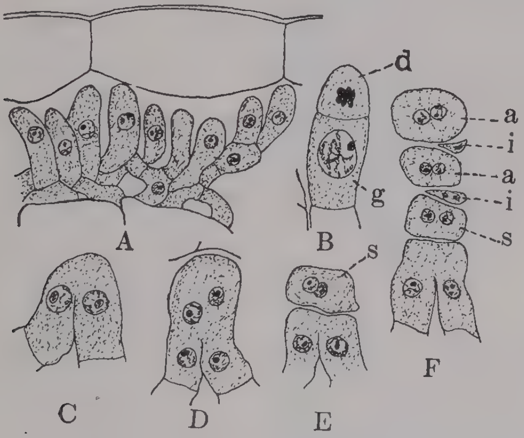

FIG. 176.—*Phragmidium speciosum* on *Rosa humilis*. Early stages in the formation of the aecium and aeciospore. A, upright hyphae under the epidermis. B, division of the end cell of a hypha into an upper, sterile, transitory cell (*d*), and a basal cell (*g*), the gamete. C, union of the two gametes. D, later stage, following first nuclear division. E, abstriction of the first aeciospore initial cell (*s*). F, row of binucleate aeciospores (*a*), separated by partly crushed intercalary cells (*i*); *s*, the last formed spore initial. (Adapted from Christman.)

divides transversely into a small lower cell, the intercalary cell, and a large upper cell, the aeciospore (Fig. 176, F, *i*, *s*). In the meantime the fused end of the two gametes increases in length, and another aeciospore-initial is cut off. It divides in turn into an aeciospore, and an intercalary cell, and the process continues, resulting in a chain of aeciospores alternating with intercalary cells. From the foregoing it is evident that the two nuclei in each are not sister nuclei, since they were derived from two separate cells regarded as gametes.

The binucleate condition of the cells of the mycelium developed from the aeciospores continues through succeeding stages until the formation of the teliospore. The teliospore initial, which is cut off from the end of an upright hypha, is binucleate. Its two nuclei divide simultaneously, the two spindles lying closely side by side. When the daughter nuclei reach their respective poles they unite, and the two spindles become as one. The division of the cell follows, giving rise to the two-celled teliospore, each cell containing a single nucleus. This condition continues until the formation of the aecium. The basidiospores developed from the teliospores are, therefore, uninucleate, and the mycelium developed from them is likewise uninucleate, i.e., haploid. The mycelium with uninucleated cells is regarded as the haploid structure; that with binucleated cells, the diploid.

The Cedar and Apple Rust.—Of the many rusts with shorter life histories, one of the best known is *Gymnosporangium Juniperi-virginianae* Schw. Two hosts are involved in the life history, but the uredinial stage is lacking. The aecia are borne on the leaves of the apple tree, or some of its near relatives as the haw (Fig. 177); the teliospores are produced on the juniper tree, more commonly known as the red cedar.

The aeciospores are carried from the apple tree to the juniper by the wind. The presence of the mycelium in the leaves of the juniper causes an hypertrophy, resulting in the formation of large, brown, leathery galls known as "cedar apples" (Fig. 178). These galls may attain the size of a hen's egg, although many remain small, and several may be found on a single twig.

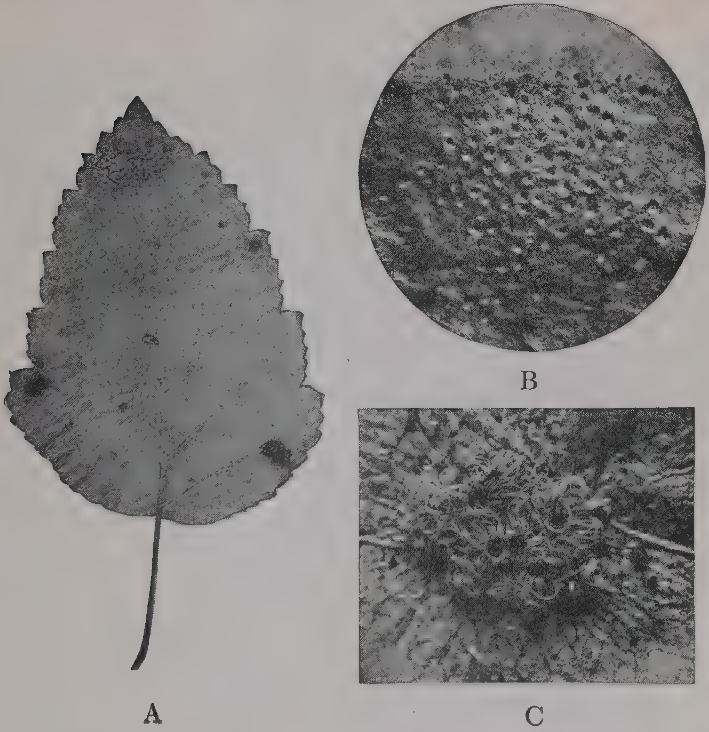

FIG. 177.—*Gymnosporangium Juniperi-virginiae.* A, leaf of wild crab apple showing spots of infection. B, diseased spot as seen from the upper side of leaf, showing openings of the pycnia. C, open aecia as seen on lower side of leaf.

In the "cedar apple" which is composed of large, thick-walled cells of cedar tissue, the mycelium spends the winter. The numerous small depressions in the surface indicate the position of developing telia. The teliospores mature in the spring (April, May) and after a rain or protracted period of moist, warm weather, long gelatinous columns of teliospores grow out from these depressions (Fig. 178). One of these masses is shown enlarged in Fig. 179. The teliospores borne on long slender pedicels germinate in this jelly, and the basidiospores resulting are carried by the wind to the leaves of the apple tree.

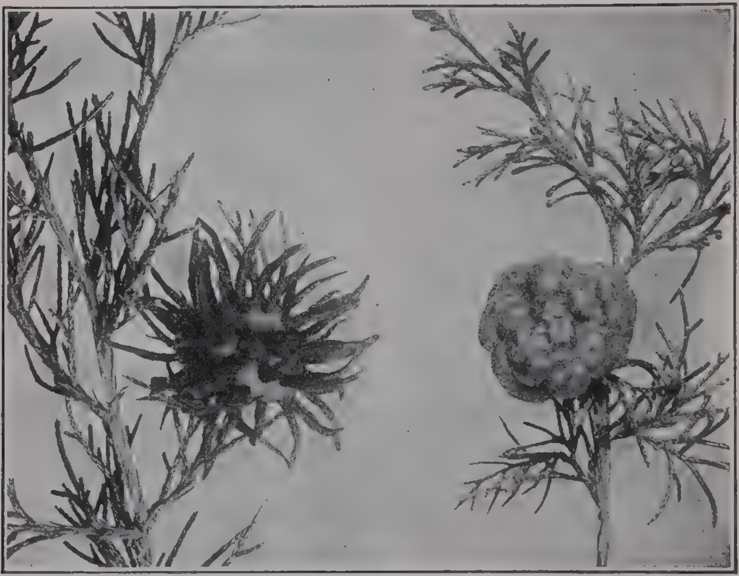

FIG. 178.—*Gymnosporangium Juniperi-virginiae.* Galls, "cedar apples" formed by the rust on leaves of juniper. At the right a "cedar apple" in winter condition. At the left, the same after the elongation of the columns of teliospores in the spring.

Some Other Rusts.—A more simple life history is seen in *Puccinia malvacearum* Mont., a rust of the common hollyhock. Only two stages occur, the telial and the basidial, and only one host is involved.

A very conspicuous rust, *Gymnoconia interstitialis* (Schlecht.) Lagerh., imparts an orange-red color to the

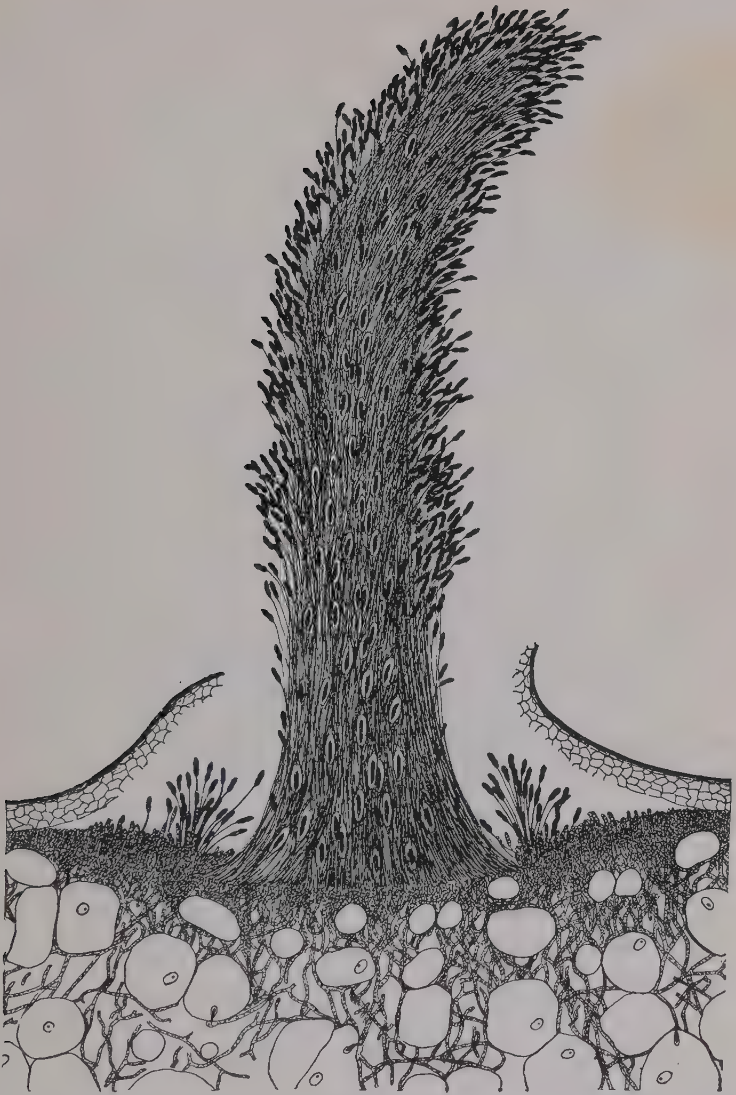

FIG. 179.—*Gymnosporangium Juniperi-virginiae.* A, longitudinal section of a column or spike of teliospores emerging from beneath the cortex of the "cedar apple." After Reed and Crabill. From Bull. No. 9 of the Virginia Agricultural Experiment Station.

leaves of the blackberry, the spore masses sometimes almost covering the lower sides of the leaves. The aeciospores here are borne in a broad cup, known as a *caeoma*, which has no definite wall of fungal tissue. The aeciospores on germination produce a structure much like a basidium, thus resembling teliospores.

The very destructive rust, *Cronartium ribicola* Fisch. de Waldh., has its aecial stage on the white pine and the uredinial and telial stages on species of gooseberry and currant.

Methods of Control of Rusts.—In order to diminish the ravages of rusts upon crop plants and forest trees various methods have been employed, all of which are based upon an understanding of the complete life history of the fungus.

In species like the cedar and apple rust in which the spores produced upon one host infect some other host, the host of lesser economic importance is destroyed in a locality of greater or less extent. If the growing of apples be of greater importance in a locality than the production of cedar trees, the cedar trees may be destroyed, or, if practicable, all "cedar apples" may be gathered in autumn or winter and destroyed.

In regions where the white pine timber is cultivated extensively, the gooseberry and currant bushes are destroyed. In like manner the destruction of the tall barberry in regions where this shrub is infected by the rust, has done much to lessen the damage caused by the parasite and to increase the yield of wheat.

In case the parasite cannot be destroyed or its dispersal be prevented, the remaining hope is to produce by breeding more resistant varieties of the desired crop plants.

There still is much to be learned concerning the rust fungus, that even beginners may think about. For example, why is the tall barberry so susceptible to infection by *Puccinia graminis* while the Japanese barberry is immune? Digging up tall barberry bushes will not alone solve the rust problem.

The Field Mushroom (*Psalliota campestris*).—The field or meadow mushroom is representative of a large class of typical basidiomycetes. The entire plant body of the mushroom, like other fleshy fungi, consists of two parts, the *vegetative mycelium* living in the substratum, and the *sporophore*, or spore-producing part, which is usually found above the surface of the substratum (Fig. 180).

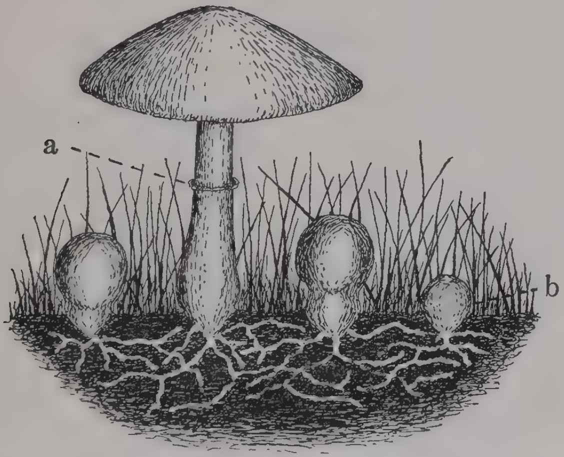

Fig. 180.—Diagrammatic habit sketch of field mushroom, showing the mycelium in the soil and sporophores in different stages of development; *a*, annulus; *b*, "button" or young sporophore.

The vegetative part consists of numerous mycelial strands and cords which spread among the particles of the soil, from which nourishment is absorbed.

The Origin and Structure of the Sporophore.—The young sporophore is recognized first as a small, white, opaque, undifferentiated mass of fungal filaments, which soon reveals within a differentiation of the two main parts of the adult sporophore, namely, the stalk, or *stipe*, and the cap, or *pileus*. These younger stages of development of the sporophore are often spoken of as "buttons" (Figs. 180, *b*). A longitudinal section of a "button" reveals the central stipe, bearing at the top the pileus folded down like a closed umbrella. A delicate membrane connects the edge of the pileus with the stipe. This is the annulus (Fig. 181, *a*). On the underside of the pileus are developed numerous thin, flat spore-bearing lamellae, more commonly known as the "gills."

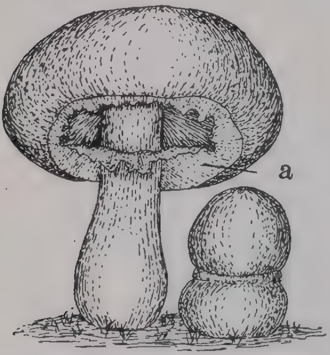

Fig. 181.

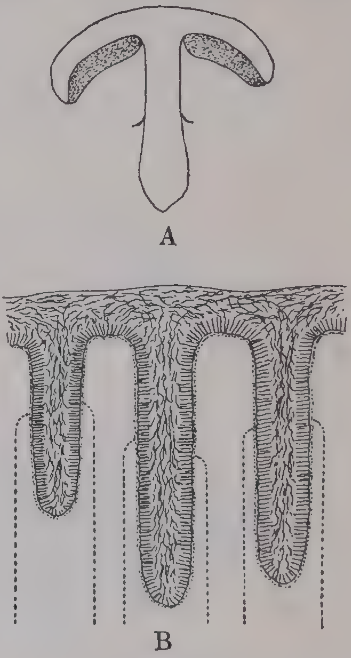

Fig. 182.

Fig. 181.—Adult sporophore and a "button" of the field mushroom (*Psalliota campestris*); *a*, annulus.

Fig. 182.—Sporophore of Field Mushroom (*Psalliota campestris*). A, longitudinal section through sporophore; the shaded parts are the "gills." B, tangential section through a portion of pileus; the dotted lines indicate the trajectories of the spores after being shot off from the basidia.

When the sporophore is mature, the stipe elongates rapidly, and the pileus opens out, the whole structure resembling an open umbrella. The annulus is broken loose from the edge of the pileus and remains as a ring around the stipe.

Viewed from the under side of the pileus, the gills are seen to be thin, flat plates radially arranged and fastened edgewise to the pileus. A tangential section of the pileus bears some resemblance to a comb, the gills corresponding to the teeth (Fig. 182, B). In a cross section of the closed pileus the gills appear arranged somewhat as the spokes in a wheel.

The stipe and pileus are composed of closely compacted hyphal filaments and closely set shorter cells that form a false tissue, *pseudoparenchyma.*

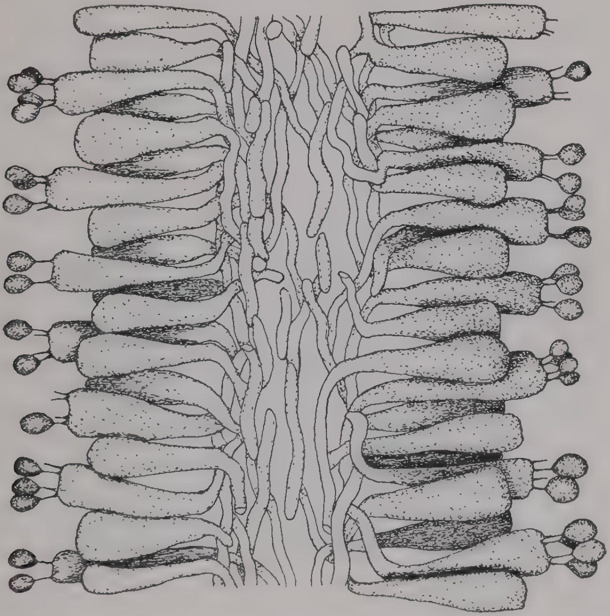

Fig. 183.—Portion of a cross section of a "gill," showing trama in the center and the hymenium on either side.

The Gill and the Hymenium.—The entire surface of the gill is covered by the hymenium; the central part of the gill is the *trama.* The relation of the two is clearly seen in a cross section, as shown in Fig. 183. The hymenium is composed of two kinds of cells, the longer being the *basidia,* and the shorter, the *paraphyses.* Each basidium bears at its free end two or more spores on slender *sterigmata.* Each basidiospore is uninucleate

(Fig. 184, E). The central part of the gill, the trama, consists of loosely interwoven, septate hyphae, most of which terminate in basidia or paraphyses.

Dispersal of Spores.—Spore dispersal in the field mushroom is accomplished by the wind. The mature spores are ejected forcibly from the sterigmata and thrown clear of other basidia. They fall freely between the gills, which are kept in a vertical position by the geotrophic response of both the stipe and the gills. The trajectories of the spores are shown by the dotted lines in Fig. 182, *b*.

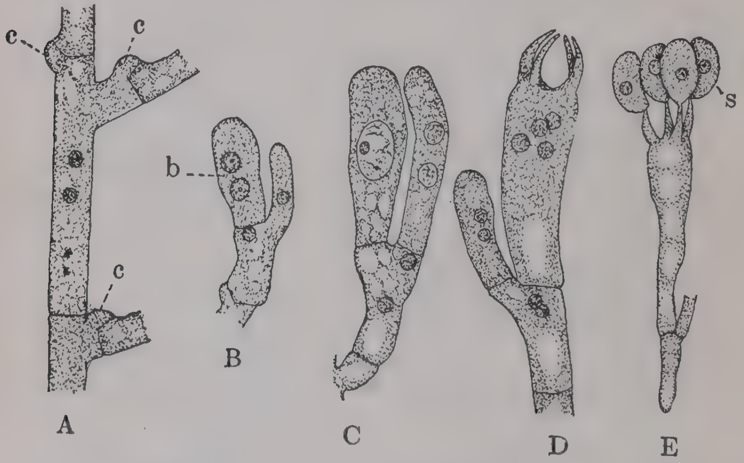

Fig. 184.—*Hypocynus· subtilis.* Clamp connections and formation of basidium. A, binucleate cell and characteristic clamp connections (*a*). B, young basidium (*b*), and a younger basidium budding out from stalk cell. C, two young basidia, in one of which the two nuclei have united. D, two basidia, the larger containing four spore nuclei and having four sterigmata already formed. E, mature basidium with four basidiospores borne on the sterigmata. (From Harper.)

Development of Basidium.—The initial cell of the basidium contains two nuclei, which soon fuse (Fig. 184, B, C). With further growth, the fusion nucleus gives rise, by two successive divisions, to four nuclei. In the meantime the four slender sterigmata have grown out of the distal end of the basidium (Fig. 184, D).

The end of each enlarges to form the sporė, into which a nucleus passes (E, *s*).

Origin of the Binucleate Cells.—The initial cells of the basidia, and the cells from which they spring, are binucleate. The mycelium developed from the basidiospores is at first uninucleate. Later in development, adjacent cells of the hyphae are united by the so-called clamp-connections, and through this connection the nucleus of one passes over into the other (Fig. 184, A).

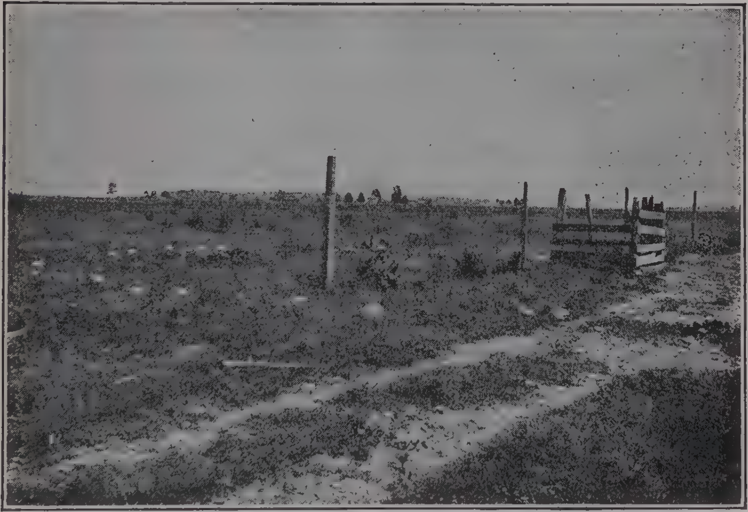

FIG. 185.—Fairy Ring of *Psalliota campestris*. (From a photograph by P. Weatherwax.)

The Fairy Ring.—In pastures and grassy fields the field mushroom and other species of mushrooms may exhibit the phenomenon known as the fairy ring. A fairy ring consists of a number of sporophores appearing above the surface of the ground in the form of a circle. The circles may vary from one-half meter or less to three or more meters in diameter (Fig. 185). Sometimes the rings form a regular and complete circle, but frequently incomplete rings result.

The mycelium of the field mushroom (*Psalliota campestris*) is perennial, living in the soil for several years. The fairy ring is, therefore, a living zone of mycelium which develops centrifugally. The actively growing outer edge of this zone develops sporophores from time to time which appear, therefore, in a ring.

It is possible that the ring of mycelium may have had its origin in a small circular area of mycelium which began to die in the center, the oldest part. Then by continued growth in a radial direction at the circumference an ever widening circle of mycelium is formed; and by continued death and decay of the older parts of the mycelium a progressively larger central area devoid of mycelium will result.

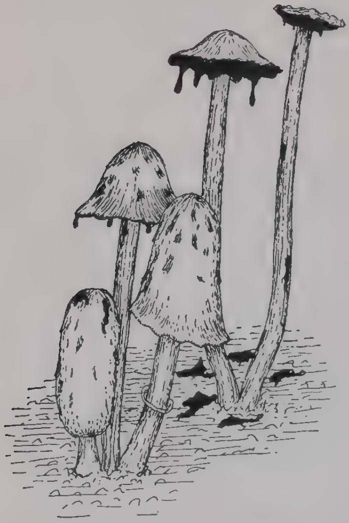

FIG. 186.—*Coprinus comatus*, Ink Horn, or Shaggy Mane mushroom; one unopened sporophore and four opened; in the mature sporophore the digested parts of the gills fall away as drops of inky-black fluid after the spores are released. The spores are dispersed by the wind.

Coprinus.—Two common mushrooms found in well fertilized lawns and fields in spring and summer are the Shaggy Mane (*Coprinus comatus*) and the Ink Horn (*Coprinus atramentarius*) (Fig. 186). These are edible if used before they turn black. In both species when the spores are mature, portions of the gills from which the spores have fallen, and the adjacent parts of the pileus undergo autodigestion, the resulting liquid falling on the ground in inky black drops. The spores ripen first at the outer ends of the gills, the process proceeding toward the stipe. The removal of the spore-free material by deliquescence facilitates dispersal, which is accomplished by the wind.

Clavaria.—The sporophore of Clavaria consists of numerous upright, somewhat club-shaped or flattened, much branched spikes, which bear the hymenium on their surfaces. The spikes are united at the base (Fig. 187).

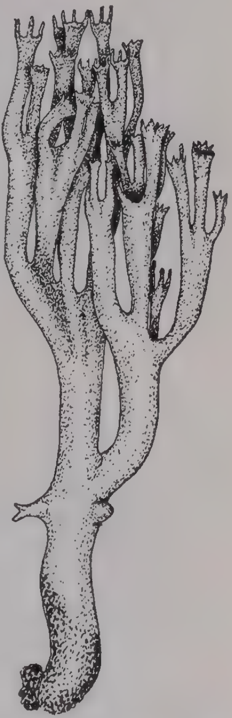

Fig. 187.—Coral Fungus, Clavaria. Portion of sporophore × 3.

Hydnum.—In the sporophore of Hydnum the spore-bearing spikes hang vertically from the pileus-like structure (Fig. 188).

Boletus.—Many species of Boletus resemble the umbrella-shaped mushrooms. Here there are numerous pores opening on the under side of the pileus. Each pore is the opening of a tube-like cavity whose inner surface is covered with the hymenium (Fig. 189).

Fomes.—The large and familiar woody shelf fungi, Fomes and Polyporus, are also pore-fungi, the pores opening on the under side of the sporophore.

Lycoperdon.—The puffballs (Lycoperdon, Calvatia) include some of the largest fleshy fungi, often measuring 40 cm. or more in diameter (Fig. 190). The spores are borne in numerous closed cavities. When mature the tissue of the sporophore dries out and the rind is ruptured or breaks off, and a slight stroke or a puff of wind will set free millions of spores, which may be blown for long distances.

Earth Star, and Bird's Nest Fungi.—Among interesting basidiomycetes of common occurrence are the species of

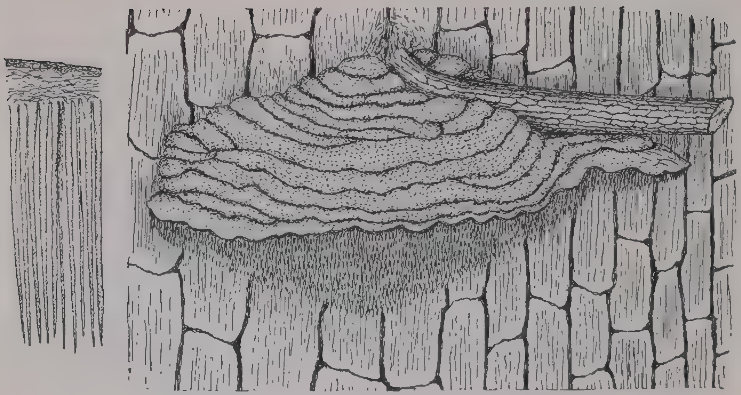

FIG. 188.—Hydnum. Sporophore attached to the bark of a pine tree. At the left a few pendant spikes enlarged.

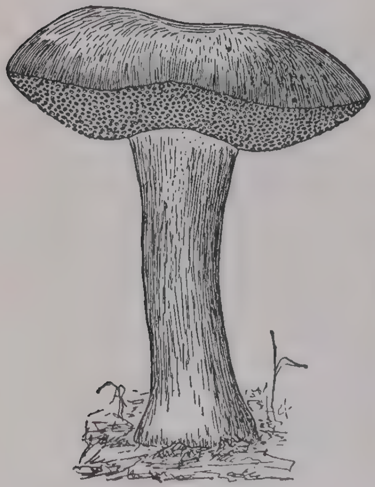

FIG. 189.—A pore-mushroom, Boletus. (From Bergen and Davis.)

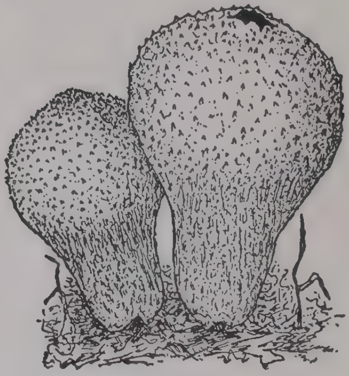

FIG. 190.—A puffiball, Lycoperdon. (From Bergen and Davis' "Principles of Botany." By permission of Ginn & Company Publishers.)

Geaster (Earth Stars) and Cyanthus (Bird's Nest Fungi). The Earth Star develops beneath the surface of the soil or other substratum (Fig. 191). When mature the outer covering (peridium) splits radially at the top, and the segments turn back, thus exposing and lifting the spore-bearing part above the surface. In some species the spore-bearing part is prolonged at the top into a nozzle-shaped protuberance.

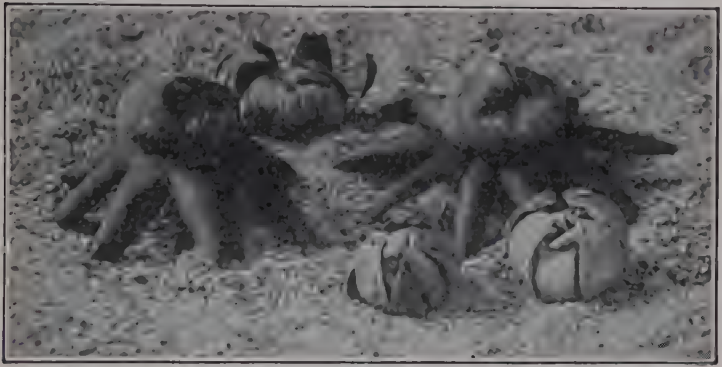

FIG. 191.—Earth Star, Geaster.

FIG. 192.—Bird's Nest Fungus.

The Bird's Nest fungus is common in summer in fields and lawns fertilized with barnyard manure and upon old sawdust. The open sporophore resembles a nest with eggs. The "eggs" are the special bodies in which the spores are produced (Fig. 192).

Stink Horn.—Perhaps the most highly specialized fleshy fungi are the Stink Horns, which owe their name to the unpleasant odor liberated when the spores are mature (Fig. 193). The spores are surrounded by a sweetish, sticky, ill-smelling fluid attractive to flies, which are among the agencies of spore dispersal.

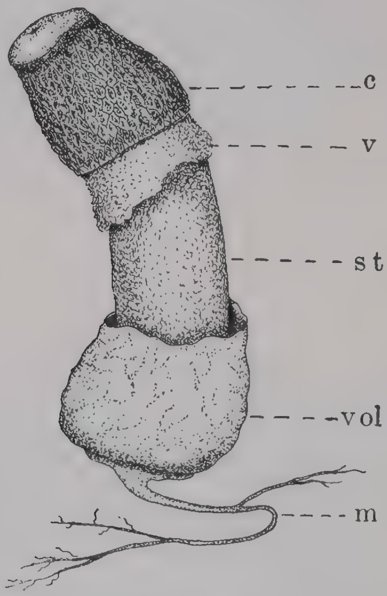

Fig. 193.—Stink-Horn or Carrion Fungus (*Dictyophora duplicata* (Bosc.) Fischer). Adult sporophore with small portion of underground mycelial cord, *m*; *st*, stipe; *vol*, volva; *v*, velum; *c*, cap.

Fungi Cultivated by Ants.—Certain species of tropical or subtropical ants of America are known to cultivate and propagate fungi as a source of food in the cavities of their subterranean nests. They prepare the substratum for their mushroom beds wholly or in part from organic material brought in from the outside. This often consists of bits of material cut from the leaves of trees and carried long distances.

Not only do the ants care for the fungi within the nest, but they establish new gardens by planting mycelium in new nests. When the young queen leaves the parental nest to start a new colony she takes with her a small pellet of living mycelium mixed with scrapings from her body. After preparing a small cavity in the ground and closing the entrance, she starts a new fungus garden and begins to lay eggs. When the larvae are large enough to need food, the mycelium has made sufficient growth to support them.

The insects apparently do not permit the fungi to form sporophores, but encourage the development of the mycelium. Tiny, knob-like proliferations, consisting of the enlarged and rounded ends of hyphae, are the parts used for food. Sporophores found in a deserted nest have made it possible to identify the fungus cultivated by one genus of ants as the Basidiomycete, *Rozites ganglyophora.* That this is the species used for food is evident from the fact that spores from this mushroom gave rise to mycelia similar to that found in the nests of the ants.

CHAPTER XV

BRYOPHYTA

The Bryophytes comprise those plants commonly known as liverworts and mosses. They stand out in striking contrast with the algae and fungi in the ease and clearness with which the haploid and diploid individuals of the life cycle may be recognized. Here the haploid individual is called the *gametophyte,* and the diploid, the *sporophyte.*

The gametophyte is, as a rule, larger and of longer duration than the sporophyte; in certain species it may live for many years. The gametophyte is also the self-nourishing individual; it bears the gametes and nourishes the sporophyte. In form the gametophyte is either a leafy stem or a flat thallus.

The sporophyte, on the contrary, is, as a rule, the smaller individual, living wholly or in a large measure, as a parasite on the gametophyte. It originates from the zygote, bears one crop of spores, and then dies. The gametophyte, which originates with the spore, may produce from one to many sporophytes, and, in case it lives from year to year, may bear a number of sporophytes each year.

The alternate succession of gametophyte and sporophyte in the complete life cycle has long been referred to as the *alternation of generations.*

HEPATICAE, LIVERWORTS

PORELLA

As an illustration of the life history of a typical liverwort, one of the larger leafy forms, Porella, may be used. The plant is found commonly on the shaded sides of tree trunks near the ground, where the moisture is more constant, and on rocks where similar conditions prevail. Some species are aquatic, at least for the larger part of the year, growing in cool, rapidly flowing water.

The Gametophyte.—The gametophyte of Porella is a leafy stem, branching monopodially (Fig. 194). With age the basal and older part of the plant dies and decays, while growth may continue at the distal ends, or growing points, for a long time, or indefinitely. The gametophyte is dorsiventral; i.e., it has a distinct upper (dorsal) and under (ventral) side. The dorsal side is always turned toward the light, while the ventral side faces the substratum. The stem bears three rows of leaves, two rows on the dorsal side, and one row on the ventral side. The upper leaves overlap like the shingles of a roof. On the ventral side of the stem is borne a single row of small leaves. The dorsal leaves are two-lobed, the smaller lobe being concealed by the upper. When the leaves are much crowded, as in the younger parts of the plant, the aspect of the under side is that of three rows of leaves. This is because the lower lobes of the dorsal leaves are of about the same size as the ventral leaves (Fig. 195, *a*, *b*, *c*).

Whitish rhizoids (brown in older parts) fasten the plant to the substream. These are neither conspicuous nor abundant.

Porella is dioecious. The female plants may be recognized by the presence of one or more small brownish structures (Fig. 194, *b*), resembling a tiny flower, the mature *sporophytes*, springing from small, bud-like branches. If such a *younger* bud be opened, the younger sporophyte will be seen as a small green knob (Fig. 197, A). The male plants are recognized by their smaller lateral branches with smaller and more closely

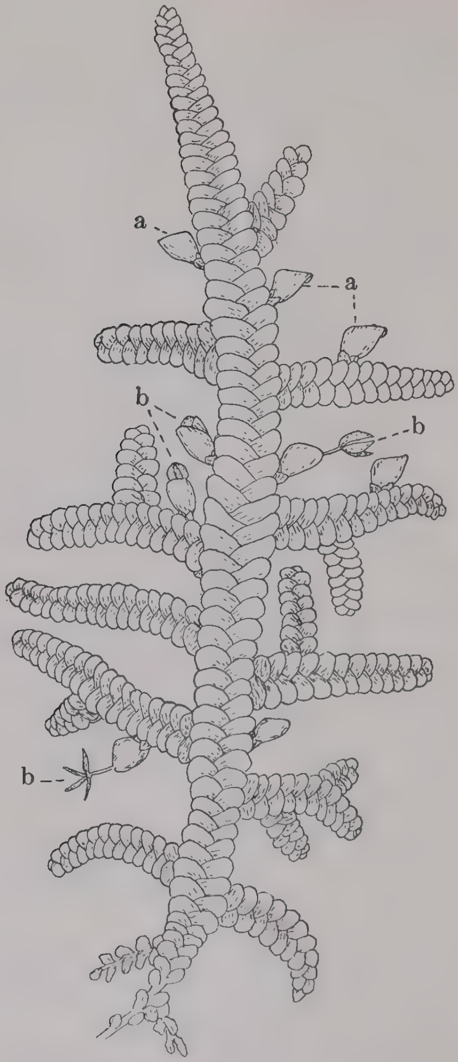

FIG. 194.—*Porella navicularis.* Part of a femile gemetophyte, seen from the dorsal side, showing arrangement of upper leaves, mode of branching, and several short, bud-like branches, *a*, with sporophytes in different stages of development, and *b*, mature sporophytes with opened capsules.

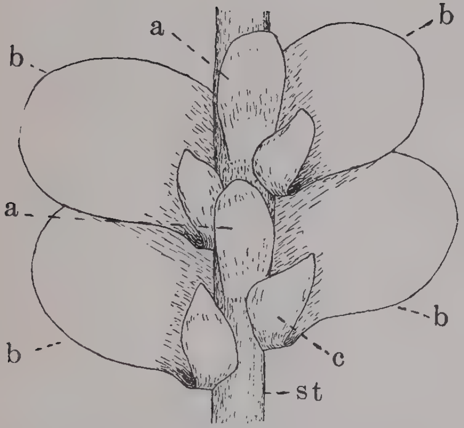

FIG. 195.—*Porella navicularis.* Small part of gametophyte seen from the ventral side. *a*, leaves attached to ventral side of stem; *b*, upper lobes of dorsal leaves; *c*, lower lobes of dorsal leaves; *st*, stem.

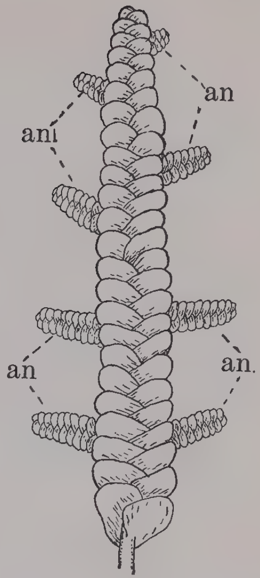

FIG. 196.—*Porella navicularis.* Dorsal view of branch of male gametophyte, showing antheridial branches, *an*.

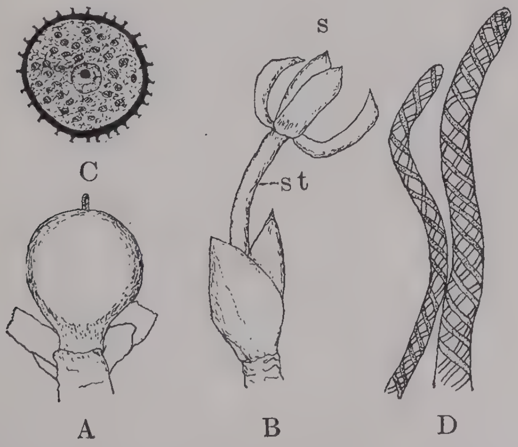

FIG. 197.—*Porella navicularis.* A, end of dwarf branch, with leaves removed, showing sporophyte still enclosed by the calyptra. B, fully matured sporophyte with open sporangium, from which spores and elaters have fallen. C, section of spore. D, portions of two elaters.

imbricated leaves (Fig. 196). These branches bear the antheridia.

The Sporophyte.—The sporophyte consists of a terminal, globular *sporangium* or capsule, a *stalk*, and a *foot* (Fig. 197, B). The capsule opens by four valves, liberating two kinds of cells, globular *spores*, and long, tubular *elaters* (Fig. 197, C, D). Each spore has a firm cell wall, provided externally with numerous very small conical thickenings somewhat hooked at the tip. The fresh spores reveal green chloroplasts. The elaters are slender, tubular cells, with two or more spiral thickenings on the inner surface. The mature elaters are devoid of living substance. In a comparatively short time after the sporangium opens the sporophyte dries out and falls away.

Structure of the Gametophyte.—The leaves of Porella are one cell thick, and without a midrib. Each cell is uninucleate, and possesses a number of chloroplasts. Sometimes cells are present containing chiefly a brown oily substance.

The stem consists mostly of elongated, thin-walled cells. The growing point of the stem terminates in an apical cell, which is tetrahedral, or in the form of a triangular pyramid, with the base representing the free outer surface. By division, cells are cut off from the three lateral surfaces. Two of the cutting surfaces of the apical cell face toward the dorsal side, while the third looks toward the ventral side of the gametophyte. Each cell thus cut off from the apical cell may give rise to a leaf, with the result that three rows of leaves are developed, two on the dorsal, and one on the ventral side.

Vegetative Propagation of the Gametophyte.—The older, or basal parts of the gametophyte die and decay, isolating the branches, which may continue to grow at the tip, thus becoming separate individuals.

The Antheridium.—The antheridia are borne in, or slightly above the axils of the small, closely imbricated leaves of the special branches mentioned above (Fig. 198, A). Each antheridium consists of a globular body and a short, slender stalk. The wall of the antheridium is three cells thick below, and one cell thick above. Within is a large number of very small cells, which give rise to the sperms. Each sperm is a cell so transformed as to be capable of locomotion in water (Fig. 198, C). It is a spirally twisted body bearing two cilia at the slender anterior end. The thicker posterior part consists largely of the condensed nucleus, while the anterior end is a very delicate thread, the *blepharoplast*, which bears the two long cilia. A vesicle may adhere to the posterior extremity.

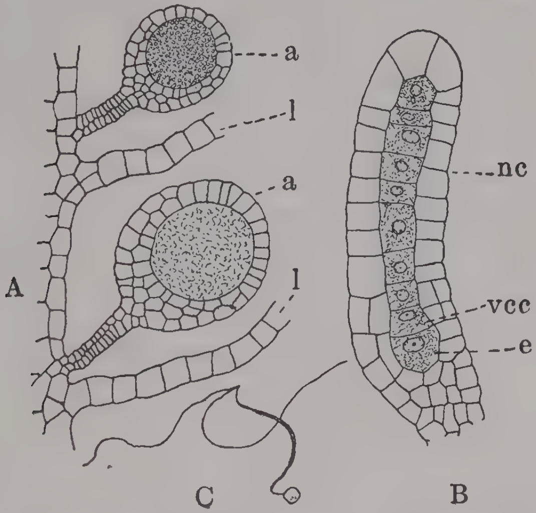

Fig. 198.—*Porella bolanderi.* Antheridium and archegonium. A, longitudinal section of two antheridia of different ages, showing manner of attachment to stem, only the epidermis of the stem being drawn; *l*, leaves; *a*, antheridia. B, longitudinal section of archegonium; *e*, egg; *vcc*, ventral canal cell; *nc*, neck canal cells. C, sperm. (A, from Bergen and Davis' "Principles of Botany." By permission of Ginn & Company, Publishers. C, from Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers.)

The Archegonium.—The oögonia, here designated as *archegonia*, are borne in terminal clusters on very short branches, which in younger parts of the plant are partly concealed by the dorsal leaves. On older parts such branches appear as small buds as stated in the foregoing. The archegonium is a flask-shaped organ having a short stalk (Fig. 198, B). The lower, enlarged, part is the *venter;* the upper part is the *neck.* As will readily be seen the organ consists of an axial row of cells, shaded in the figure, surrounded by an outer layer of cells. The outer layer, or wall, of the neck is one cell thick, while that of the venter may be two cells in thickness. The lowermost cell of the axial row (*e*). is the egg. The cell just above the egg is the ventral canal cell (*v cc*), and the remainder are the neck canal cells. The egg and ventral canal cell are sisters in origin.

Both the antheridia and the archegonia originate each in a single epidermal cell, but their development is too complicated to be discussed here.

The Process of Fecundation.—As the archegonium reaches maturity the neck canal and ventral canal cells are disorganized into a mucilaginous substance. If water be now applied to the ripe archegonium, the neck opens at the top, and some of the mucilaginous material is expelled and begins to diffuse in the water. The egg remains in the venter.

As the antheridium ripens, the walls of the sperm-bearing cells likewise change into a mucilaginous substance. When wetted with water the ripe organ opens and the sperms are set free. They swim about actively in the water derived from rain or heavy dew in their native habitat. When the sperms are sufficiently near the opening of the neck of the archegonium, they enter and pass down to the egg. The entire sperm enters the cytoplasm of the egg, and finally its nucleus fuses with that of the egg. The fecundated egg, or zygote, now begins its development into the sporophyte. It is evident, therefore, that the cells of the sporophyte will have the double number of chromosomes.

The Development of the Sporophyte.—Soon after fecundation the neck of the archegonium shrinks and turns brown, but the venter continues growth as a cover for the sporophyte. The sporophyte reaches maturity within the enlarged venter of the archegonium, which is now called the *calyptra*.

The form and general structure of the sporophyte, and its relation to the end of the stem bearing it, will be made clear in Fig. 199, which is a view of a longitudinal section. The nearly mature sporophyte is differentiated into three regions, namely, the rounded upper end (*sp*), the *sporangium*, the constricted middle part (*st*), the *stalk*, or *seta*, and the expanded lower end, the foot (*ft*). The foot absorbs water and food from the stem of the gametophyte.

Within the sporangium two kinds of cells are differentiated, long, slender cells (*el*) that develop into elaters, and globular spore mother-cells (*smc*). The spore mother cells soon become four-lobed and give rise each to a tetrad of spores. In the formation of the tetrad from the mother-cell, two nuclear divisions characteristic of spore mother-cells in the higher plants take place. The first of these mitoses is a reducing division by which the number of chromosomes is reduced one half. The second is an equational division. Every spore possesses, therefore, the single (haploid) number of chromosomes. The spore is, then a one-celled gametophyte; all cells of the gametophyte, which comes from the spore, contain the single number of chromosomes.

The sporophyte reaches maturity within the calyptra. The stalk then elongates, and the sporangium is forced out through the ruptured wall of the calyptra and beyond the enveloping leaves of the bud. The capsule

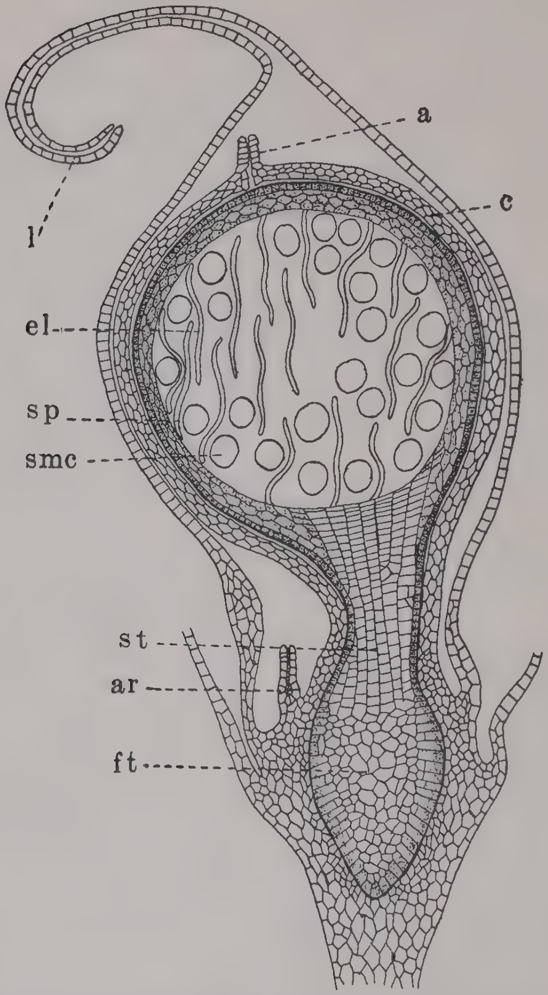

FIG. 199.—*Porella navicularis.* Longitudinal section through a dwarf branch with immature sporophyte enclosed within the calyptra; *a*, neck of archegonium; *c*, calyptra, enlarged venter of archegonium; *st*, stalk; *ft*, foot; *el*, elaters; *sp*, sporangium; *smc*, spore mother cell; *ar*, archegonium; *l*, enveloping leaves.

opens by four valves, and spores and elaters are set free. As the elaters dry, they twist and become entangled in masses of varying sizes. In each tangle of elaters may be held several to many spores. The spores and elaters are scattered chiefly by the wind. When the mass strikes a moist surface, the elaters straighten out and free the spores, which may adhere to the substratum. The elaters are effective in the deposition of spores in groups. Since about one half of the spores are potentially male, and the other half potentially female, gametophytes of both sexes are enabled to develop together on a very small area.

Summary of the Life History of Porella.—From the foregoing we have learned that the sporophyte is derived from the union of egg and sperm. It reaches maturity within the calyptra, deriving nearly all of its nourishment from the gametophyte. The sporophyte lives, therefore, parasitically on the gametophyte. After the spores are developed the sporophyte dies. Spores grow into gametophytes.

MARCHANTIA

As a representative of a liverwort in which the gametophyte is a flat, ribbon-like thallus, we shall select the well known and beautiful *Marchantia polymorpha.* It may be found in moist, shady places on the ground, not infrequently near the foundation on the shaded sides and walls of buildings. In cultivation it grows well on coal ashes or on earth.

The Gametophyte.—The gametophyte is in the form of a flat, ribbon-like, fleshy, deep green, dorsiventral thallus, which branches dichotomously. Each branch is traversed by an inconspicuous midrib, which leads to a growing point located in a notch or depression at the distal end of the branch (Fig. 200, A). The upper, or dorsal surface is marked by polygonal areas generally rhombic in outline (B). Near the center of each area is a stoma leading to a cavity beneath the epidermis. Each cavity is as large as the rhombic area, and is separated from similar neighboring cavities by partitions generally one cell in thickness. These partitions beneath the epidermis correspond to the boundaries of the areas as seen externally. Along the margin in fresh and rapidly growing plants may be seen a row of small pinkish scales.

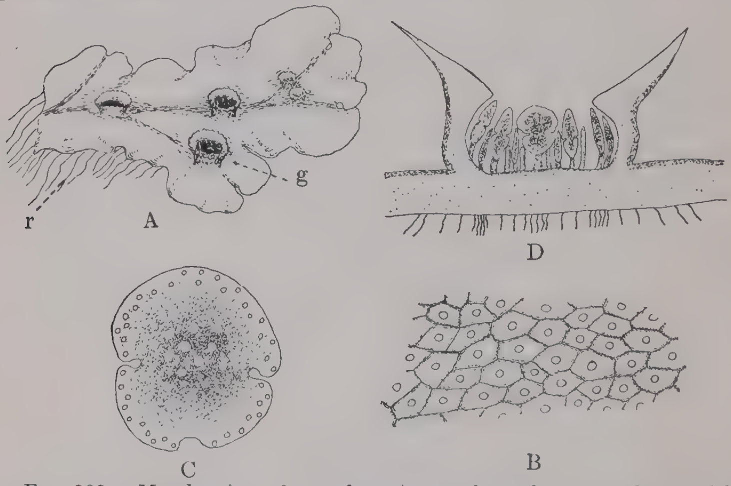

FIG. 200.—*Marchantia polymorpha.* A, portion of gametophyte with gemma cups, *g*; *r*, rhizoids. B, several rhombic areas of the dorsal surface of the thallus. C, a gemma. D, diagram of vertical section of gemma cup, showing manner in which gemmae are borne.

From the lower epidermis of the thallus are developed numerous unicellular rhizoids, which fasten the plant to the substratum and absorb water (*r*). The rhizoids are of two kinds: those springing from the midrib are large and smooth-walled (Fig. 201, B); those arising on either side of the midrib are smaller and have undulating walls with peg-like thickenings projecting into the cavity of the cell. In some rhizoids the thickenings are small and conical; in others they are large and irregular in shape (Fig. 201, C, D).

Along the midrib on the under side are also two rows of minute scale leaves that originate at the growing point (Fig. 201, *l*). These are not readily seen even with the aid of a pocket lens. They serve to protect the tender cells of the growing point from too rapid desiccation, and probably from mechanical injury. On the younger scale leaves overlapping the growing point are glandular hairs which secrete a mucilaginous substance.

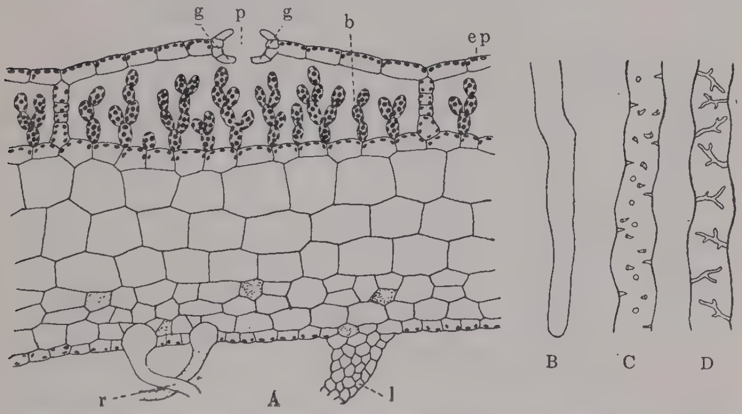

Fig. 201.—*Marchantia polymorpha.* Structure of the thallus. A, vertical section showing one large air-cavity beneath the epidermis. *g*, guard cells; *p*, pore of stoma; *b*, chlorophyll-bearing cells; *ep*, epidermis; *r*, rhizoids; *l*, scale leave. B, C, D, portions of each of three kinds of rhizoids, the last two with inner thickenings of the wall.

Vegetative Propagation.—The gametophyte of Marchantia propagates vegetatively in two ways: by the death and gradual decay of older parts, by which branches are disconnected; and by means of specialized shoots known as *gemmae*. The gemmae are borne in small cups on the dorsal surface (Fig. 200, A, *g*). Each gemma is a flat, rounded structure with a basal scar indicating the place of attachment to the short stalk on which it was borne, and with two notches indicating the growing points.

From the bottom of the cup spring also short glandular hairs which secrete a mucilage. By the swelling of this mucilage, and by the growth of young gemmae beneath, the mature gemmae are detached (D). Eventually they are scattered by rain, and in favorable localities begin to grow in two directions into new plants. Both sides of the gemma are alike, and that which happens to be next to the substratum becomes the ventral, and the other the dorsal, side of the thallus. Gemmae are produced in great numbers during the earlier vigorous vegetative period of growth, before the appearance of the sex organs.

Structure of the Thallus.—The details of structure of the adult thallus may be readily understood from a transverse vertical section (Fig. 201, A). Along the dorsal side are the large air-chambers roofed over by the epidermis. From the floor of each air chamber arise cactus-like clusters of thin walled cells containing many large chloroplasts (A, *b*). These cells constitute the principal photosynthetic tissue of the plant, although a few smaller chloroplasts are present in the epidermis and in other parts of the thallus. The pore is surrounded by a structure resembling a chimney, or a barrel with the ends removed (*p*). This structure consists generally of four tiers of cells, each tier being made up of four cells forming a ring. The four cells of the inner tier are larger, and constitute the guard cells, which tend to open and close the pore (*g*).

The tissue below the layer of air chambers is composed of large and nearly colorless cells. Here and there among these may be found certain cells filled with mucilage, while others contain an oily substance. The epidermis on the under side is made up of smaller cells with few chloroplasts. From the epidermal layer near the growing point the rhizoids and scale leaves arise.

The Growing Point.—The growing point terminates in one or more initial cells known as apical cells, from which all parts of the plant are primarily derived. Each apical cell is wedge-shaped, and divides by cutting off new cells alternately from the dorsal and ventral faces.

The Sex Organs.—Marchantia is dioecious, but male and female plants cannot be distinguished as such before the appearance of the specialized branches that bear the sex organs. The archegoniophore consists of a slender, upright stalk bearing a conspicuous terminal star-shaped structure (Fig. 202, A). The antheridiophore has a similar stalk, bearing at its upper end a circular disk with a lobed margin (B). The structure of both the archegoniophore and the antheridiophore is similar to that of corresponding parts of the flat thallus.

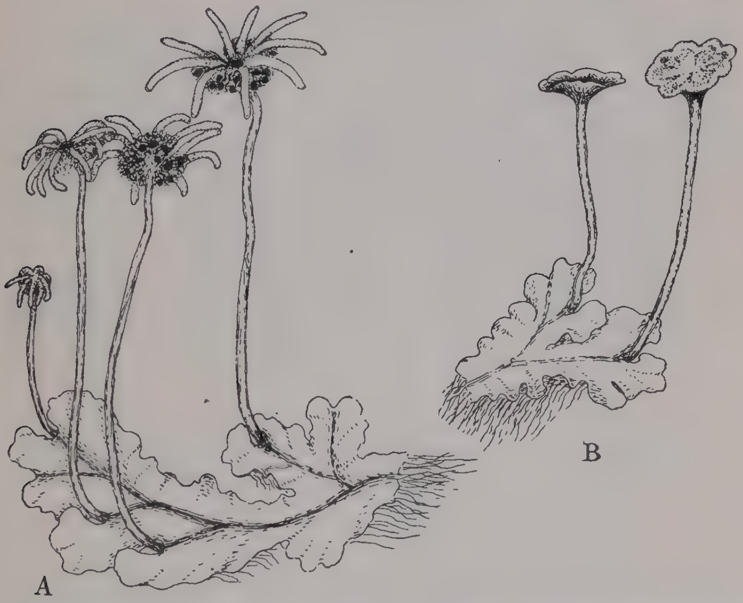

Fig. 202.—*Marchantia polymorpha.* A, portion of female gametophyte with archegoniophores in different stages of development. B, portion of male gametophyte with antheridiophores.

The archegonia originate in the notches between the rays of the star-shaped structure, just back of the growing points. They appear to be on the lower side, but arise really on the morphological upper side, which becomes turned under by the peculiar growth of the disk.

The archegonium is similar to that of Porella, namely, flask-shaped, and consisting of a central row of cells surrounded by a wall one row of cells in thickness. The lowest cell of the central row is the egg, the one next above it the ventral canal cell, and the remainder the neck canal cells (Fig. 203, B, *a*, D).

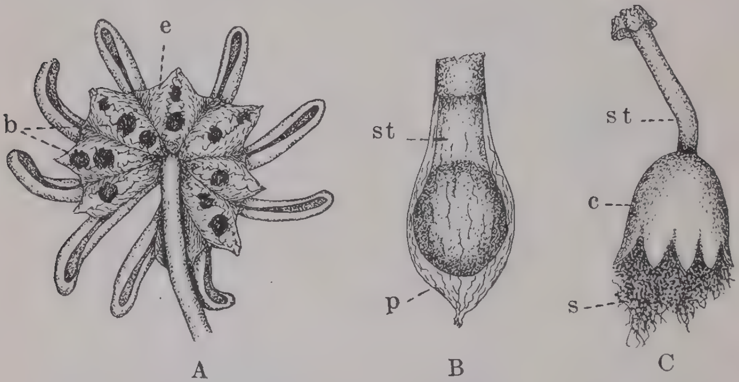

FIG. 203.—*Marchantia polymorpha.* A, underside of archegoniophore, showing sporophytes, *b*, in position; *e*, perichaetium. B, mature but unopened sporophyte within the perianth, *p*. C, opened mature sporophyte. *st*, stalk; *c*, sporangium (capsule); *s*, mass of spores and elaters.

The antheridia are located in flask-shaped cavities in the upper surface of the antheridial disk (Fig. 202, A, *an*). Each is a slightly elongated body with a short stalk (Fig. 203, C). The wall consists of a single layer of cells. Each small cubical cell within the body of the antheridium gives rise to two sperms after undergoing a diagonal division. The sperm is similar in structure to that of Porella.

Fecundation and Development of Sporophyte.—When the sex organs are ripe they open on the application of water. The sperms ooze out on the surface of the antheridial disk in small drops of mucilaginous substance and are scattered by raindrops. If the water containing sperms falls on an unexpanded archegonial disk (Fig. 202, A) it will flow down between the rays and be drawn by capillarity to the archegonia, bringing the sperms to the open necks. The mucilaginous substance derived from the neck canal cells exerts a chemotactic stimulus upon the sperms, and they enter the archegonia, and one finally unites with the egg.

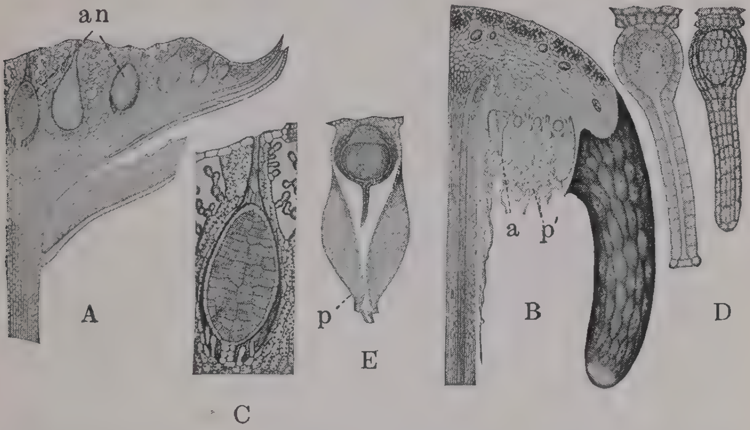

Fig. 204.—*Marchantia polymorpha.* A, Vertical section of one half of an antheridiophore, showing antheridia, *an*, embedded in cavities in the dorsal surface. B, similar section through one half of archegoniophore; *a*, archegonium; *p′*, perichaetium; C, antheridium more highly magnified. D, archegonium in external view and in section. E, young sporophyte enclosed in calyptra and surrounded by the perianth, *p*. (After Kny.)

The fertilized egg, or zygote, immediately begins to develop into the sporophyte. The younger stages of the sporophyte are spoken of as the embryo. The embryo is globular at first, but later becomes pear-shaped (Fig. 204, E). The sporophyte reaches maturity within the venter of the archegonium, which keeps pace with the growth of the former and becomes the *calyptra* as in Porella (E). In the nearly mature sporophyte three parts are recognized: the rounded *capsule*, the stalk, or *seta*, and the *foot*, which fastens the sporophyte to the tissue of the gametophyte and absorbs food and moisture from it.

During the development of the sporophyte there grows up around the archegonium, from its base, an enveloping membrane one cell in thickness. This envelope has been called the *perianth*, or *pseudo-perianth* (Fig. 204, E, *p*). The second membrane surrounding the group of sporophytes developed between any two finger-like rays of the archegonial disk is called the *perichaetium* (Fig. 203, A, *e* and Fig. 204, B, *p*′). It has a fringed or lacerated edge.

Morphologically the archegonial disk represents a set of branches, the spaces between the rays representing the midribs. Each midrib, except the one representing the stalk of the archegoniophore, bears a row of archegonia surrounded by the perichaetium.

As in Porella, two sorts of cells are ultimately formed in the capsule, namely, spores and elaters (Fig. 203, C, *s*). When the sporophyte is mature the stalk elongates greatly, forcing the sporangium out through the ruptured calyptra and beyond the opening of the surrounding perianth and perichaetium (Fig. 203, A, *b*). The sporangium or capsule now opens and the spores are dispersed by the wind.

Classification of Liverworts

The known species of liverworts may be grouped under two classes, the Hepaticeae, typical liverworts, and the Anthocerotes, horned liverworts.

Class I. The typical liverworts may be included in the following orders and families. Under each family will be given some of the genera commonly met with.

Ord. 1. Marchantiales.

Fam. Ricciaceae.—Sporophyte consisting of only a capsule. A rudimentary foot may be recognized in early stages of certain forms. No elaters are present.

Riccia, Ricciocarpus

Fam. Marchantiaceae.—Sporophyte with a stalk and a capsule of about equal length. Elaters are present.

Marchantia, Lunularia, Reboulia, Conocephalus (Fegatella), Fimbriaria

Ord. 2. Jungermanniales.

Fam. Jungermanniaceae.—Sporophyte with stalk three or more times the length of the capsule. Elaters present.

Thallose forms (Anacrogynae) Pellia, Aneura, Metzgeria, Pallavacinia

Foliose forms (Acrogynae) Porella, Frullania, Lejeunia

Class II. Anthocerotes.—The Anthocerotes, or horned liverworts, differ so fundamentally from the rest of the liverworts that the author has followed the suggestion of Campbell and has placed these plants in a separate class. In the deep-seated archegonia and antheridia, and in the early development of the sporophyte these plants resemble more closely such lower ferns as Ophioglossum and Botrychium. A further diagnosis is given in a following paragraph.

Fam. Anthocerotaceae

Anthoceros, Notothylus, Dendroceros

Ricciaceae

The genera Riccia and Ricciocarpus are commonly spoken of as the mud-flat liverworts because of their occurrence on muddy flats, on the firm, moist banks of streams, and in similar localities. Some species, as *Ricciocarpus natans*, grow as floating aquatics, as well as on the ground.

The gametophyte is a dichotomously branched, dorsiventral thallus, frequently forming circular, rosette-like expansions a centimeter or more in diameter (Fig. 205, A). A single row of scales developing on the lower side of the thallus later split in the middle to form two rows. Rhizoids are developed in the terrestrial forms but not in the floating forms. The midrib and ventral region are composed of closely arranged cells, while the dorsal region is usually very loose and spongy, owing to the presence of numerous intercellular spaces of varying size, many of them becoming large air chambers. Many of these air spaces are in communication with the outer air by means of pores in the epidermis.

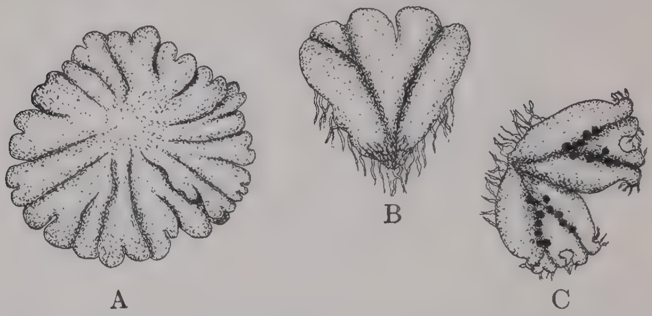

Fig. 205.—Riccia and Ricciocarpus. A, habit of *Riccia Frostii* Aust. B, C, floating form of *Ricciocarpus natans*, the latter (C) bearing a row of sporophytes along each midrib.

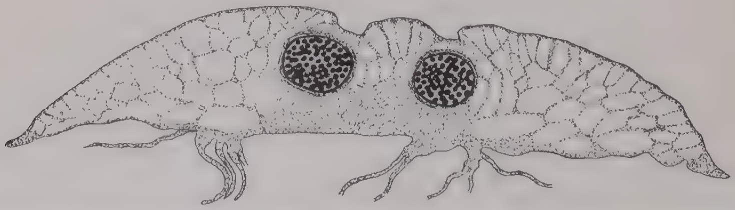

Fig. 206.—*Ricciocarpus natans*. Diagram of cross section of thallus, showing sporophytes embedded in midrib.

The antheridia and archegonia are embedded in the tissue of the midrib on the dorsal side, being developed from superficial cells just back of the growing point.

The sporophyte, which is also embedded in the tissue, consists of merely a capsule, or a capsule and a poorly developed foot (Fig. 206). No elaters are present. The spores are set free after the thallus dies and decays. As stated in a preceding paragraph, species of Ricciocarpus live as terrestrial forms and as floating aquatics. On solid earth the rosettes are larger and characteristically smooth and trim in appearance, while as a floating aquatic no rhizoids are developed, but numerous scales on the ventral side become very large and conspicuous (Fig. 205, B, C).

MARCHANTIACEAE

In addition to the well-known Marchantia, the genera Conocephalus (Fegatella), Reboulia, Fimbriaria, and Lunularia are commonly met with.

Conocephalus conicus Dum. (*Fegatella conica* Corda.) is probably the largest of our liverworts. It grows abundantly on moist, shady earth, and especially on limestone ledges that are quite moist for a large part of the year. The gametophyte resembles that of Marchantia with the exception that the rhombic areas on the dorsal surface are larger and more conspicuous. The plant gives off a characteristic odor. The antheridiophore is sessile, resembling a wart-like structure just back of the growing point (Fig. 207, B). The archegonial disk is conical, without the finger-like rays as is Marchantia, and it is mounted on a long slender stalk when the sporophytes are mature (Fig. 207, A). The stalk is very short until the sporophytes are nearly mature. The sperms are forcibly discharged from the antheridium. In greenhouse cultures, if the antheridial plants are sprinkled with water, especially after their surfaces have become somewhat dry, tiny volleys of mist will be shot up from antheridiophores, which mushroom out in still air like smoke from a volcano, and fall on any archegonial disk that may be near (Fig. 207, B). Mature fruiting specimens may be found in February and early spring.

Reboulia hemispherica Raddi (*Asterella hemispherica* Beauv.) grows on earth and limestone in relatively dry places. The ventral surface is purple with a row of scales on each side of the midrib. The archegonial disk is conic-hemispheric, becoming flattened above, and usually four-lobed.

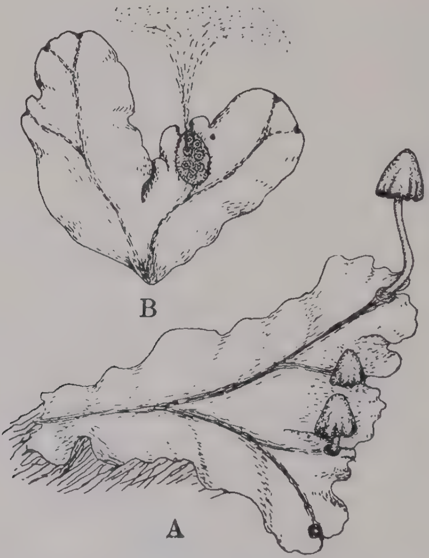

FIG. 207.—*Conocephalus conica* (*Fegatella conica*). A, portion of gametophyte with archegoniophore bearing sporophytes. B, portion of gametophyte with a sessile antheridiophore from which sperms are being forcibly discharged.

Fimbriaria tenella Nees resembles Reboulia in some respects. The gametophyte has the midrib thickened into a keel. The two rows of scales beneath are purple. The archegonial disk is conic or hemispheric, bearing usually four sporophytes, which are surrounded by a fringed envelope. The plant is monoecious. Lumularia is chiefly a greenhouse form, recognized by the crescent-shaped gemma cups.

JUNGERMANNIACEAE

In such representatives of the thallose Jungermanniaceae as Pellia, Aneura, etc. the gametophyte is a flat, dorsiventral thallus, smaller and much simpler in structure than the Marchantiaceae. In *Pellia epiphylla* Raddi, for example, the sex organs are immersed in the thallus. When mature, the sporophyte consists of a long colorless seta, with the terminal, globular capsule opening by valves (Fig. 208).

The leafy Jungermanniaceae are typified by Proella, which is, however, a relatively large form. Frullania, Lejeunia, etc. are relatively small and inconspicuous, growing on logs and tree trunks. A species of Proella found in Indiana is aquatic. It grows attached to limestone in cool, rapidly flowing water.

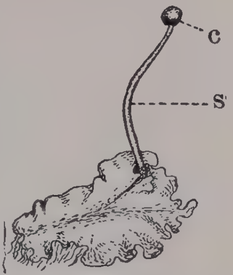

FIG. 208.—*Pellia epiphylla.* Gametophyte bearing mature sporophyte. *c*, capsule; *s*, stalk or seta.

ANTHOCEROTACEAE

Of the three genera of the Anthocerotaceae, namely, Antoceros, Notothylas, and Dendroceros, the first two are native to our flora, and the third is tropical.

Anthoceros.—The gametophyte of Anthoceros is a small, dark green, dorsiventral thallus, branching dichotomously or irregularly and forming rosettes from one-half to one or more centimeters in diameter. The irregular edges often obscure the growing points (Fig. 209, A). Delicate rhizoids fasten the plants to the soil.

The thallus is simple in structure, being composed of rather uniform cells that form a compact tissue. In some cases intercellular spaces are present, some of which contain a mucilaginous substance. Except in a tropical form, each cell possesses a single large characteristic chloroplast with a pyrenoid.

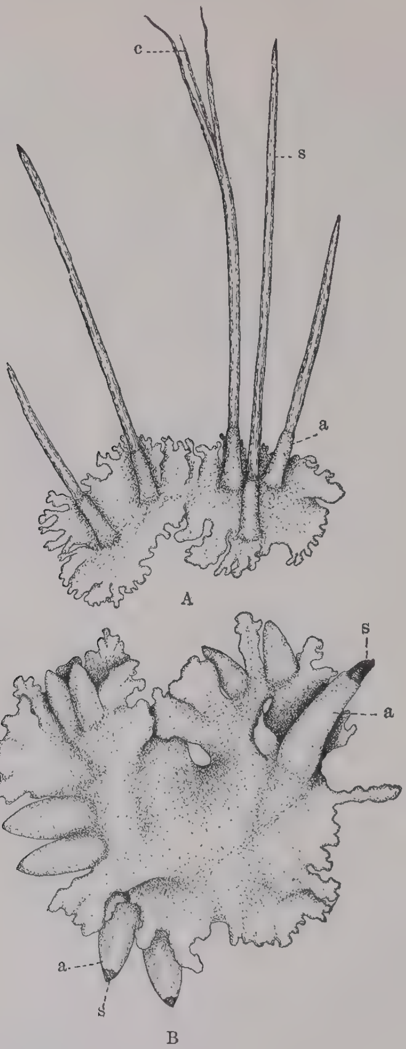

Fig. 209.—*Anthoceros punctatus* and *Notothylas orbicularis*. A, gametophyte of *A. punctatus* bearing several sporophytes in different stages of development, the oldest one having opened by a longitudinal slit, and showing the columella between the two valves; × 6. *c*, columella. B, gametophyte of *N. orbicularis*, with several almost horizontal sporophytes. *s*, sporophyte; *a*, sheath at base of sporophyte; × 10.

Here and there in the thallus may be seen dark, blue-green specks, which are colonies of Nostoc. The alga gains entrance through small mucilage slits on the under side just back of the growing point. The Nostoc colonies are not always present. They do not seem to be of any value to the Anthoceros, nor do they cause any injury. The growth of the thallus, as in Notothylas, proceeds from one or more wedge-shaped apical cells (Fig. 212, A, *a*).

The Sporophyte.—The sporophyte differs very greatly from that of any other class of liverworts, and, because of this fact, the Anthocerotaceae are of special interest from the standpoint of the evolution of the liverworts, and from the light that they throw on the origin of the lower ferns.

The mature sporophyte is cylindrical, and may attain a length of several centimeters. Sporophytes may be developed in considerable numbers on a given rosette, when they often suggest a very small tuft of grass (Fig. 209, A). They reach maturity outside the venter, being green in color, and not wholly dependent upon the gametophyte for nourishment. The tissue of the gametophyte grows up about the base of each sporophyte forming a sort of sheath (Fig. 209, *a*). The cells of the outer part, or the wall, contain chloroplasts, one in each cell in *Anthoceros laevis* and *A. punctatus*. Stomata similar to those of higher plants are present in the epidermis.

The sporophyte does not, as in other liverworts, consist of a seta and capsule, in which the spores all mature at the same time. On the contrary, the spores mature a few at a time, but continuously throughout the life of the sporophyte.

The structural plan of the sporophyte is illustrated in Fig. 210, which is a diagram of a longitudinal section. The lower end consists of the bulbous foot, (*f*) which is embedded in the tissue of the gametophyte. Extending up through the center is the columella (*c*). Surrounding

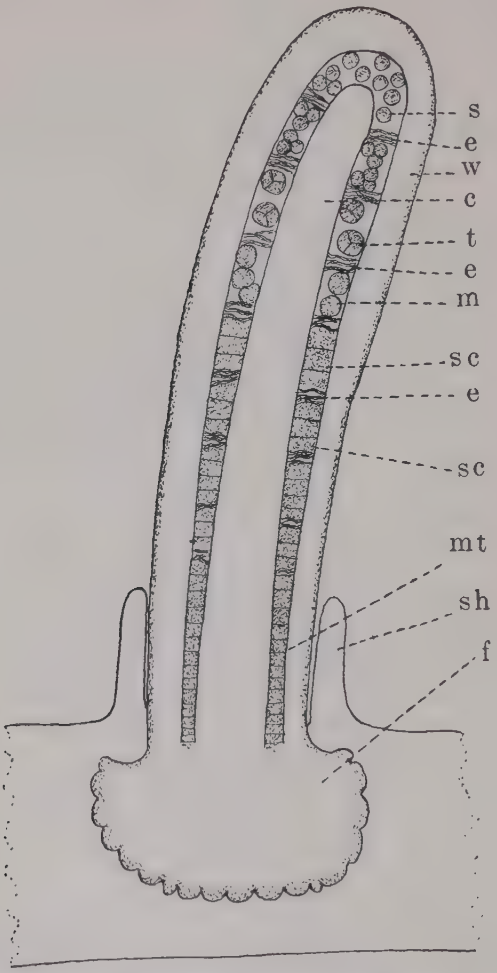

FIG. 210.—Anthoceros. Diagram of longitudinal section of sporophyte. Explanation in text.

the columella is the spore-bearing region, several cells in thickness, which extends over the upper end of the columella. The meristematic region is just above the foot (*mt*). The wall of the sporophyte is several cells in thickness. In the spore-bearing region, from the growing zone upwards, smaller sterile cells (*e*), which will give rise to elaters, alternate with larger cells (*sc*) that will produce the spores. Beginning with the tip of the sporophyte, we find first mature spores (*s*) followed downwards by spore tetrads (*t*), both being interspersed with the rudimentary elaters; below the tetrads come the spore mother cells (*m*), and below these, alternating layers of spore-bearing and sterile cells. The structure of the lower part of the sporophyte is accurately shown in Fig. 211, A and B, which pertains to Notothylas, whose sporophyte is similar to that of Anthoceros. In Fig. 211, A, we have the large bulbous foot (*a*), with the outer

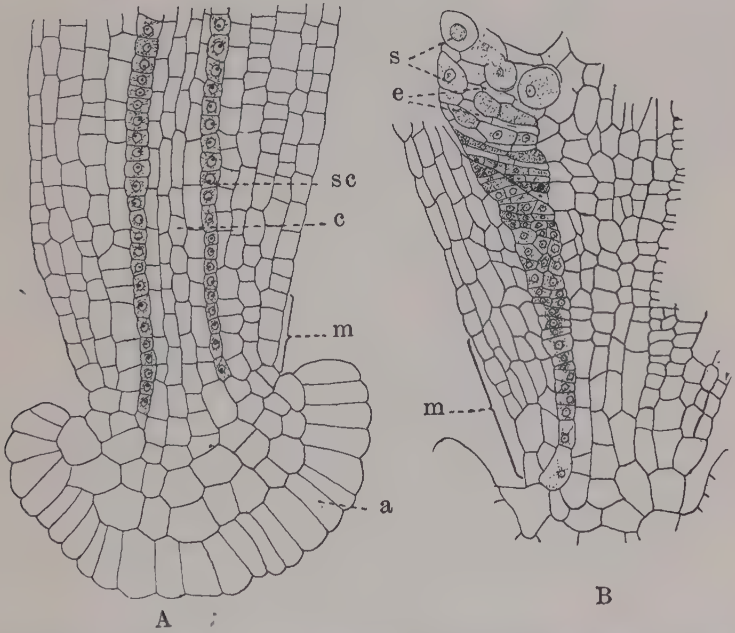

Fig. 211.—Notothylas. A, longitudinal section through base of young sporophyte. B, longitudinal section of one half of base of older sporophyte. *a*, foot; *m*, meristematic region at base of sporophyte; *c*, columella; *sc*, sporogenous tissue; *s*, spore mother cells; *e*, elaters. (After Mottier.)

layer of cells somewhat elongated. Above the foot is the meristematic zone (*m*), showing differentiation of spore-bearing cells (*sc*), and the columella (*c*) in the center. Fig. 211, B is a median longitudinal section of a part of the base of an older sporophyte, in which the successive layers of the sterile and spore-bearing cells are accurately shown, together with their origin in the meristematic region. The sporophyte of Anthoceros continues growth and spore production until the death of the part of the gametophyte that produced it, or until cold weather brings the life of the plant to an end.

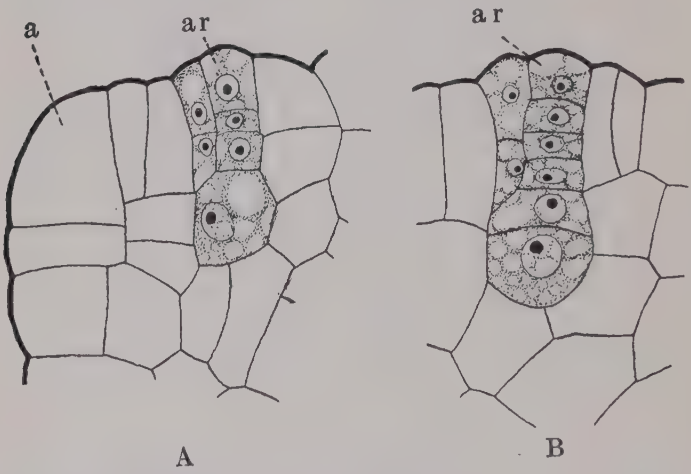

FIG. 212.—*Notothylas orbicularis.* Growing point and archegonia. A, longitudinal section through growing point of thallus. B, archegonium almost mature. *a*, apical cell; *ar*, archegonium.

The Sex Organs.—The antheridia and archegonia of Anthoceros and Notothylas are quite similar in structure and development. The antheridia arise in closed cavities beneath the epidermis (Fig. 213). The archegonium arises from a surface cell, but the mature organ is embedded in the tissue. The terminal cells of the neck may, however, project above the surface (Fig. 212, A, B).

Notothylas.—The gametophyte of Notothylas resembles that of Anthoceros, though it is usually smaller. The sporophyte is smaller, and it does not grow upright into a slender thread. After breaking through the calyptra, it curves forward and comes to lie horizontally on the thallus Fig. 209, B). In general the sporophyte is similar in development to that of Anthoceros. The meristematic growth at the base is much less extensive, however, than in Anthoceros. Although the spores are developed first at the tip of the sporophyte, this structure

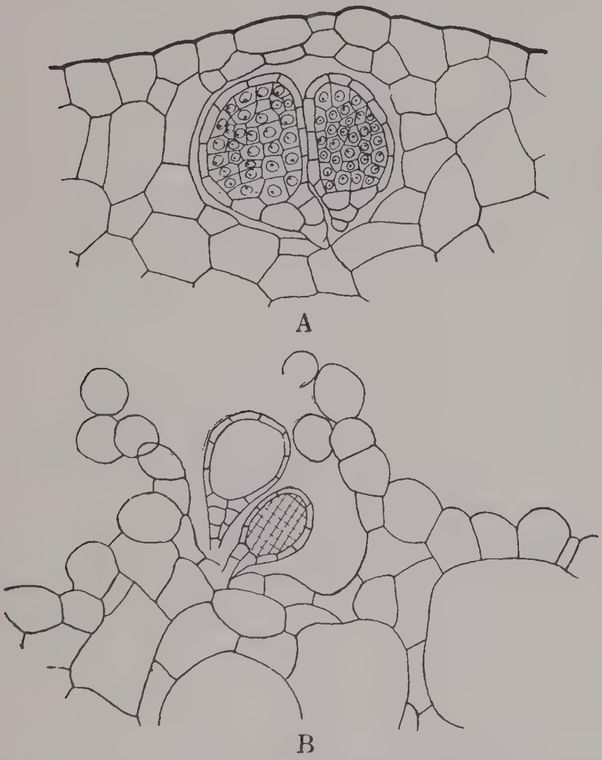

Fig. 213.—*Notothylas orbicularis.* A, vertical section of thallus, showing two antheridia in closed cavity beneath upper surface of gametophyte. B, section showing manner of opening of antheridial cavity.

does not open until a large majority of the spores are mature. There is formed, therefore, a capsule which resembles somewhat that of the other liverworts. The wall of the capsule does not develop photosynthetic tissue, and stomata are not present.

When the spores are mature, the cells at the base of the capsule elongate and finally break away from the foot, thereby severing all connection with the latter.

Continuity of the Chloroplast in Gametophyte and Sporophyte.—In a preceding paragraph attention was called to the presence of one large and characteristic chloroplast in each cell of the gametophyte and sporophyte of *Anthoceros laevis* and *A. punctatus*. In the spore mother-cell one chloroplast is present. During the division of this cell to give rise to the tetrad, the chloroplast undergoes two successive divisions, as does the nucleus. Each spore is consequently provided with a chloroplast, and this condition is maintained in each cell throughout the gametophyte. However, in the development of the sperm the chloroplast disappears, with the result that no trace of a chloroplast is found in connection with the mature sperm. In the egg, on the contrary, a chloroplast is present, though somewhat reduced in size, and from this the chloroplast of the sporophyte is derived. In other words, the sporophyte inherits its chloroplast through the egg alone.

Evolution of the Sporophyte in Liverworts.—When the structure and development of the sporophyte of the liverworts is taken into consideration, one finds a very noticeable series of progressive changes from the Ricciaceae to the Jungermanniaceae. In the Ricciaceae, which have the simplest sporophyte, this structure consists of but a sporangium or capsule. Foot and seta are lacking, or the former may be present in a rudimentary state. The first step in progress above this simple sporophyte is seen in Marchantia, in which about one-half of the sporophyte (the distal half) becomes the capule, the other half giving rise to the foot and the seta. One-half of the sporophyte has become vegetative (sterile) tissue. In the Jungermanniaceae progressive sterilization has proceeded much farther, from about two thirds to three fourths being vegetative tissue. In these three families the sporophyte is almost wholly dependent upon the gametophyte.

When we come to the Anthocerotes, we find that progressive differentiation has gone much farther. There is first the large foot, then the meristematic region just above it, by which the mass of the sporophyte is increased, and finally the presence of a central strand of vegetative tissue, the columella. Added to these features we have the development of photosynthetic tissue, which is a long step toward the independence of the sporophyte. Further evidence of continued growth and greater independence of the sporophyte has recently been brought to light in a Californian species, *Anthoceros fusiformis* Aust., in which the sporophyte may attain a length of 16 centimeters. In this species the foot has been found to have become exposed, owing to the disintegration of the cells of the gametophyte. Under such circumstances it is possible that the foot may be able to absorb water from the soil.

In the liverworts the capsule of *Notothylas orbicularis* is intermediate between the type of the ordinary liverworts, the Hepaticae, and the more highly specialized spore-producing portion of Anthoceros. The sporogenous region in Anthoceros, with its alternating sections of spore-bearing and sterile cells, finds a striking parallel in the sporophore of Ophioglossum, one of the lower ferns (p. 381), in which the embedded sporangia alternate in a longitudinal series with vegetative tissue. In Ophioglossum the spores are set free through a lateral slit in each spore-bearing mass (sporangium), while in Anthoceros such is not the case. If, in Anthoceros, each spore-bearing aggregate of cells, separated by the sterile or elater-producing cells, were to open laterally by a slit to the exterior, and if the columella were to develop vascular tissue, the similarity between the sporophore of Ophioglossum and that part of the Anthoceros sporophyte above the meristematic zone would be complete.

Moreover, the embryo sporophyte of the Ophioglossaceae, with its large foot, bears a resemblance to the embryo of Anthoceros. If the meristematic zone of Anthoceros could be conceived as developing a root and a rudimentary leaf, we should then have a fern sporophyte. It is not difficult to imagine how the fern sporophyte, as it occurs in Ophioglossum, could have been derived from some ancestral form resembling the sporophyte of Anthoceros.

MUSCI. MOSSES

The mosses are much more abundant than the liverworts, and in certain localities constitute a very characteristic feature of the vegetation. The number of species is far greater than in the liverworts, but there is in general a greater uniformity in form and structure in the numerous species.

In general a moss gametophyte may be distinguished from that of a liverwort in that the former is an upright leafy stem whose spirally arranged leaves have a midrib. In some species the plants grow prostrate on the substratum and may present the appearance of dorsiventrality. The rhizoids are multicellular, consisting of branched filaments, usually with golden brown cell walls. The transverse walls of the rhizoids may be oblique (Fig. 215).

The sporophyte is larger and more highly differentiated than that of the liverworts. It consists of a long, slender *seta*, bearing at the distal end a large capsule which opens by a circular lid, the *operculum* (Fig. 214, A, *ca*, and B, *o*). Beneath the operculum in many species is a fringe of teeth which can be readily

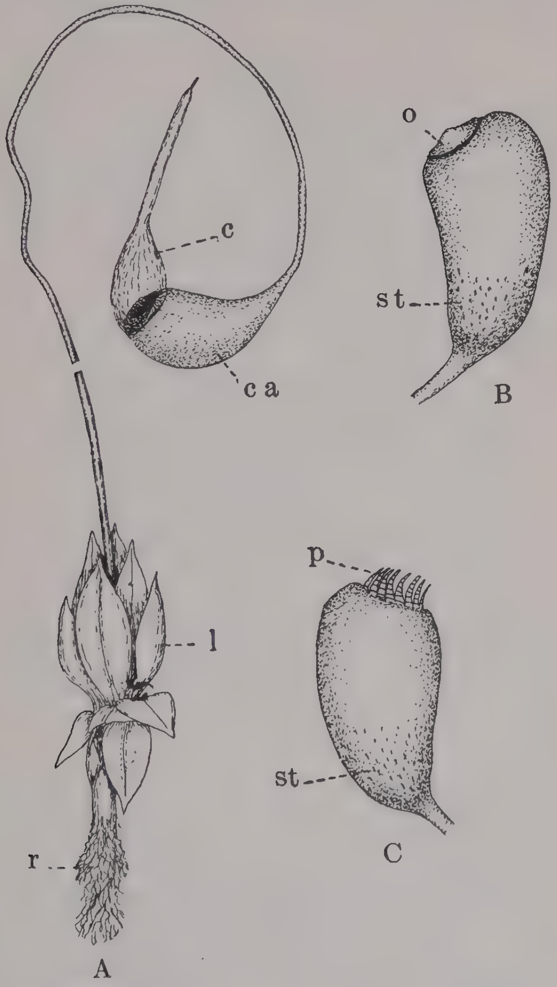

Fig. 214.—*Funaria hygrometrica.* A, entire plant, sporophyte attached to gametophyte. B, capsule of sporophyte. C, ripe capsule after the operculum has fallen off. *r*, rhizoids; *l*, leaves; *c*, calyptra; *o*, operculum; *p*, peristome; *st*, stomata on basal portion of capsule.

seen when the lid falls off (Fig. 214, C, *p*). These teeth constitute the *peristome*. The peristome may consist of a double row of teeth, referred to as the inner and outer peristome.

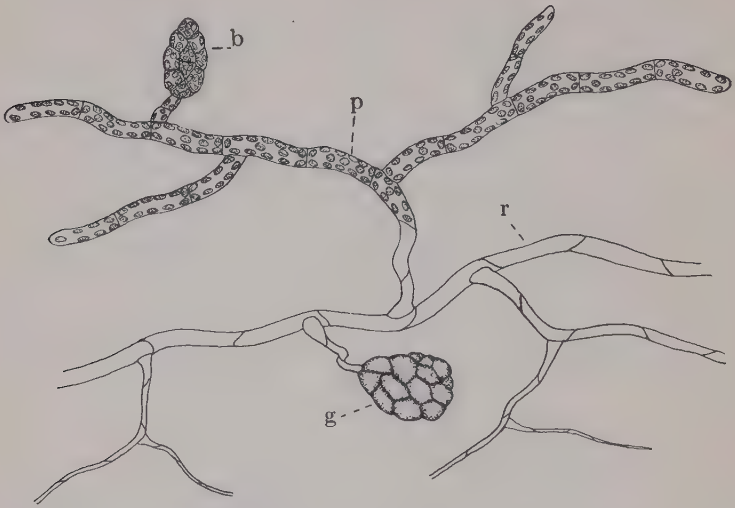

Fig. 215.—*Funaria hygrometrica.* Portion of a rhizoid, *r*, from which has grown a secondary protonemal branch, *p*; *g*, underground gemma (bud); *b*, aerial green bud, which will develop into the leafy stem of the gametophyte.

FUNARIA

The life history of a moss may be illustrated in the study of some form of simple structure, such as the common Cord Moss, *Funaria hygrometrica*. It may be found on earth, and in almost pure stands on cinders and heaps of ashes that have been left undisturbed for a season.

The complete plant is a short leafy stem fastened to the substratum by the brown rhizoids, and bearing at its upper end the sporophyte, which consists of a long, slender, brownish seta terminating in a nodding capsule. When mature the seta exhibits hygroscopic curvatures, and for this reason it may be used in the construction of simple hygrometers (Fig. 214, A).

The Gametophyte.—The upright stem of the gametophyte bears three rows of leaves arranged spirally. Each elongated leaf is pointed at the tip and possesses a midrib, the central cells of which serve as a conducting tissue (Fig. 216, B). The rest of the leaf is made up of a single layer of cells containing numerous chloroplasts.*

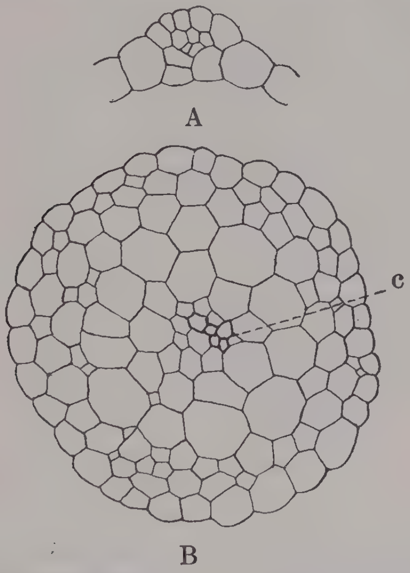

Fig. 216.—*Funaria hygrometrica.* A, cross section of stem of gametophyte. B, cross section of midrib of leaf. *c*, strand of conducting cells.

The rhizoids are branched filaments with brown walls. The cross walls are often oblique. In the rhizoids the chloroplasts are usually undeveloped, being present only in the form of primordia. On exposure to light, branches are formed having numerous chloroplasts. These branches are known as *secondary proto-*

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* The leaves of some mosses, such as Polytrichum, are more complex, in that several lamellae arise at right angles from the upper side and extend longitudinally. These greatly increase the photosynthetic tissue of the otherwise narrow leaves.

nema. They have colorless cell walls, and the transverse septa are at right angles to the longitudinal axes of the cells (Fig. 215, *p*). Primary protonema, to be mentioned in a following paragraph, arises from the spore.

As may be seen in a cross section, the stem is simple in structure (Fig. 216, A). In the center is a strand of smaller cells surrounded by cells more or less uniform in character. The cells of the central strand are much elongated; they function as conducting tissue (Fig. 216, *c*). Beneath the epidermis the cells may be smaller and have thicker walls.

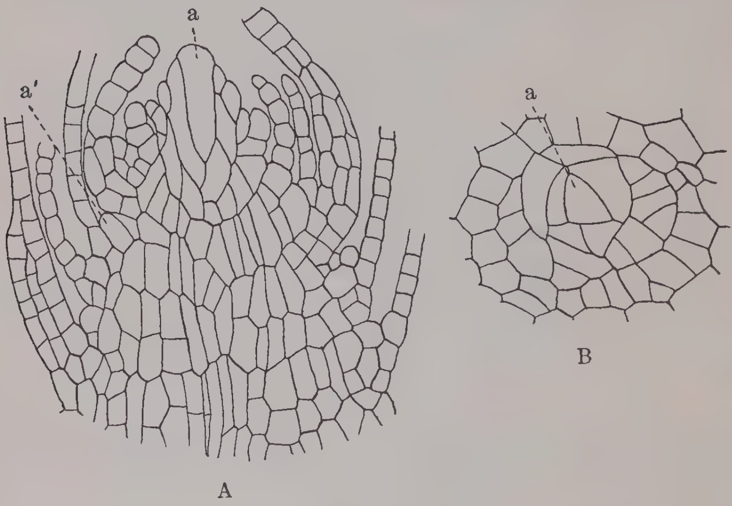

Fig. 217.—*Amblystegium riparium*, var. *fluitans*. A, median longitudinal section of the growing end of a stem. B, transverse section through the apex of a stem. *a*, apical cell; *a′*, initial cell of a lateral branch. (From Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers.)

The growth of the stem proceeds as a rule from an apical cell which is in the form of a tetrahedron, or triangular pyramid, with its free surface somewhat rounded (Fig. 217, A, *a*). In a cross section, therefore, the apical cell will appear as a triangle (Fig. 217, B, *a*).

From the three lateral faces of the apical cell are cut off by successive divisions three rows of cells, which give rise primarily to the stem and leaves. In stems that branch, each branch springs from an initial cell that arises immediately below a leaf (Fig. 217, A *a′*).

Vegetative Propagation of the Gametophyte.—As stated in a foregoing paragraph, if the rhizoids be exposed to the light, secondary protonema will be developed from certain cells (Fig. 215, *p*). On these filaments, as from primary protonema, will arise small green buds (*b*), which develop into leafy plants. The leafy stem is sometimes referred to as the gametophore. Gemmae in the form of small brown buds are sometimes formed in the same way from rhizoids beneath the soil (*g*). These are called resting buds. If exposed to the light, under growing conditions, they develop secondary protonema, from which leafy stems may spring. In some mosses gemmae are developed on the leaves. These may ultimately give rise to leafy plants. In some species the leafy stem may produce long, slender, creeping stolons with reduced leaves, and these may give rise to upright leafy stems.

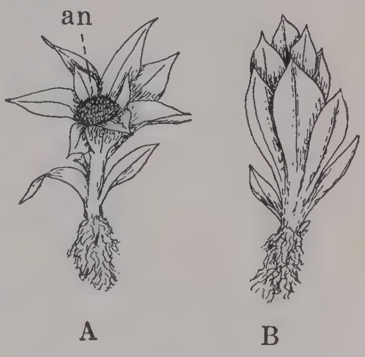

FIG. 218.—*Funaria hygrometrica.* Male and female gametophytes. A, male plant with cluster of antheridia, *an*, at tip of stem. B, female plant. The archegonia, borne also at the tip of the stem, are concealed by the leaves. × 7.

Sex Organs.—Funaria is dioecious. The male gametophytes are smaller than the female and may be recognized by the more loosely arranged leaves and by the presence of a group of reddish antheridia at the apex of the stem and surrounded by a rosette of leaves (Fig. 218, A, *an*). The antheridia are more clearly seen in a longitudinal section of the tip of the stem (Fig. 219, *a*, 220, A).

Each antheridium is club-shaped, possessing a short stalk. The wall consists of a layer of relatively large cells that may contain reddish bodies. Within is a large number of very small cells which give rise to the sperms. The latter are similar to those of the liverworts (Fig. 220, D). When the mature antheridium becomes wet the sperms are expelled in a mucilaginous substance derived largely from the walls of the sperm-bearing cells.

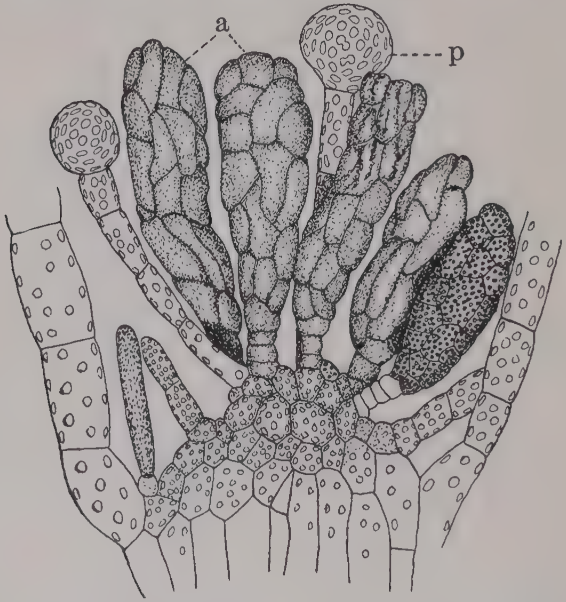

FIG. 219.—*Funaria hygrometrica.* Longitudinal section through tip of male plant, showing antheridia, *a*, and paraphyses, *p*. (From Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers.)

The female plant is larger than the male and has larger and more closely set leaves (Fig. 218, B). The archegonia are flask-shaped like those of the liverworts, though much larger. They are borne at the apex of the stem (Fig. 220, B). In monoecious gametophytes, the antheridia and archegonia may be borne together in the same cluster.

Fecundation and Development of the Sporophyte. The processes involved in the opening of the archegonium and in the union of egg and sperm are the same as in the liverworts.

The embryo sporophyte grows rapidly into a long, slender rod and severs the archegonium from the stem (Fig. 221, A-D). The wall of the archegonium, now known as the *calyptra* (*c*), is carried on the distal end of the sporophyte. The sporophyte, at this stage, appears to the unaided eye as a slender thread arising from the end of the gametophyte. With further growth the distal end of the sporophyte, which is covered by the calyptra, enlarges greatly and becomes differentiated into the capsule (D, *b*). In Funaria the calyptra may fall off before the capsule is mature.

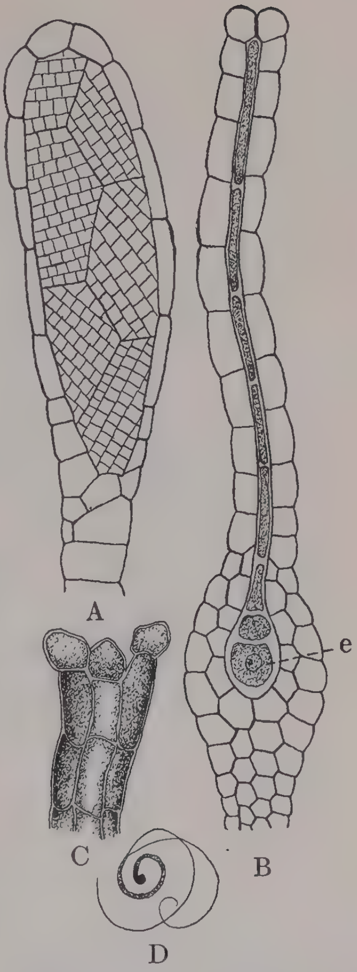

Fig. 220.—*Funaria hygrometrica.* Sexual organs. A, longitudinal section of immature antheridium. The small cubical cells give rise to the sperms. B, median longitudinal section of mature archegonium; *e*, egg. D, surface view of distal end of archegonial neck, showing manner of opening. D, sperm. (A, D from Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers. B, C from Goebel.)

Beneath the calyptra is seen the lid or operculum (Fig. 214, B, *o*). When the operculum falls off, the peristome is seen as a fringe of triangular, brown teeth, as mentioned in a preceding paragraph. The peristome of Funaria is double, the inner being inconspicuous. The teeth of the outer peristome represent strips of cell wall conspicuously marked by horizontal thickenings (Fig. 222, B, *o*). In the Hairy-Cap Moss, *Polytrichum commune*, each tooth of the single peristome consists of a cell. The thin gray membrane stretched across the mouth of the capsule is the *epiphragm* (Fig. 223, B, *e*).

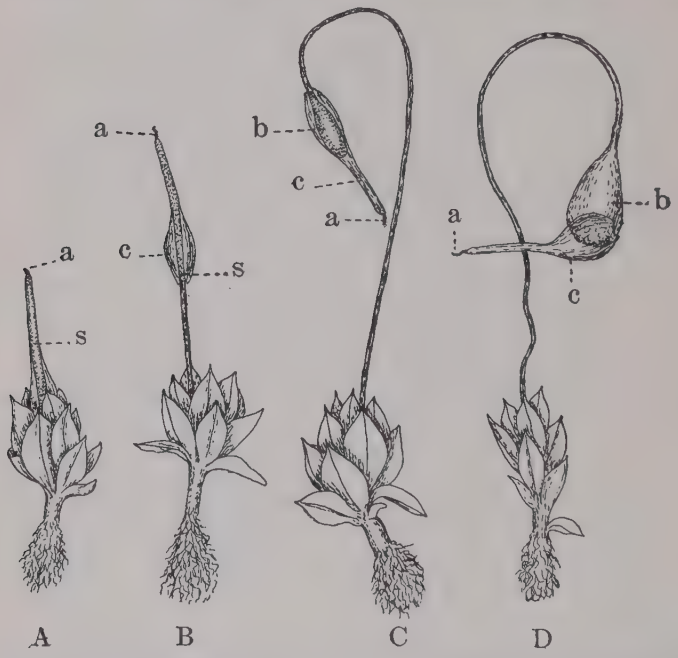

FIG. 221.—*Funaria hygrometrica.* A-D, development of the sporophyte, the capsule forming in the last two figures. *a*, shrivelled neck of archegonium; *s*, young sporophyte; *c*, calyptra; *b*, capsule of sporophyte.

Structure of the Capsule.—The structure of the capsule before it reaches maturity may be understood from a median longitudinal section (Fig. 222, A). It is seen that the capsule consists of an outer wall three layers of cells in thickness and a central mass of tissue, with a large air space between them. The central mass is continuous with the upper part of the capsule, and is connected with the wall and bottom of the capsule by slender filaments of chlorophyll-bearing cells. On either side of the inner mass, near its surface, is a row of spore-bearing tissue (*s*). The large, thin-walled cells comprising the inner part of the mass (*c*) constitute the columella. The spore-bearing layer is, therefore, in the

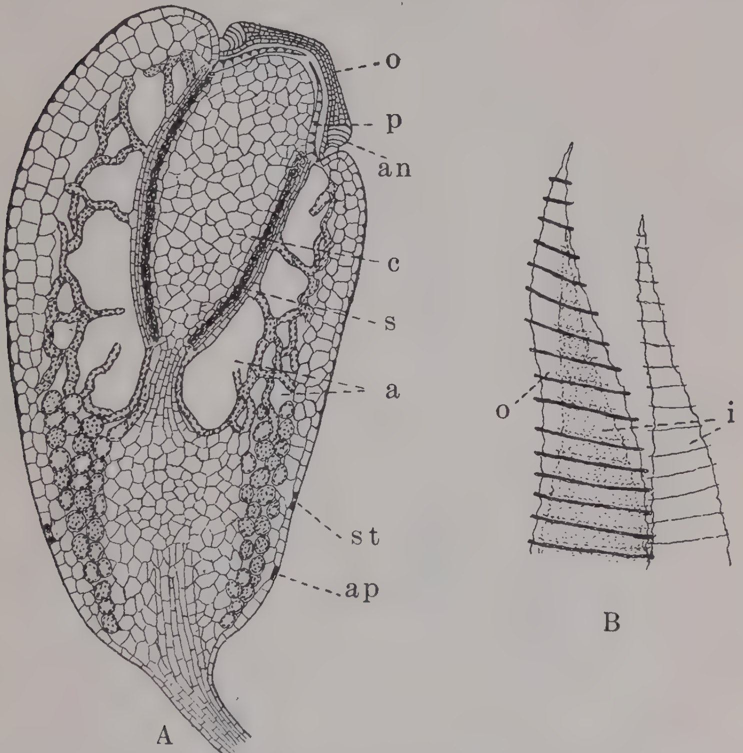

Fig. 222.—*Funaria hygrometrica.* A, longitudinal section of immature capsule of sporophyte. *o*, operculum; *p*, peristome; *an*, annulus; *c*, columella; *s*, sporogenous tissue; *a*, air spaces; *st*, stomata on apophysis. B, part of the peristome. *o*, outer peristome; *i*, inner peristome.

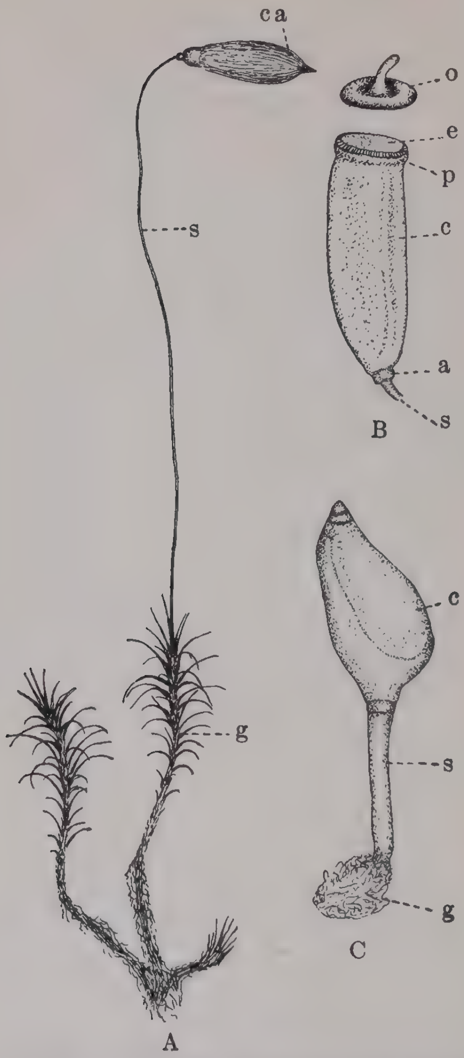

FIG. 223.—A, habit of the large, hairy-cap moss, *Polytrichum commune.* B, capsule of the same greatly enlarged. C, *Buxbaumia aphylla*, one of the small, rare, peculiar mosses. *c*, capsule; *ca*, calyptra; *s*, seta; *o*, operculum; *e*, epiphragm; *p*, peristome; *a*, apophysis; *g*, gametophyte.

form of a cylinder, with the columella extending through it above and below. Between the spore-bearing cells and the air space is a layer of tissue three cells in thickness.

The upper end of the capsule is covered by the operculum (*o*). The large, conspicuous cells (*an*) at the base of the operculum constitute the annulus. By the mechanical action of the annulus the operculum is separated from the rest of the capsule. Beneath the operculum is the peristome (*p*).

The lower part of the capsule, which narrows into the seta, is the *apophysis* (*ap*). Its loosely arranged cells contain chlorophyll and represent photosynthetic tissue. From the central part of the base of the apophysis a strand of conducting tissue extends down into the seta. The outer layer of small cells with rather thick walls is the epidermis. In the region of the apophysis stomata are present in the epidermis, forming a communication between the outer air and the intercellular spaces within the capsule.

As in Anthoceros, the sporophyte of the moss is capable of making a part of its own food, and it is therefore not wholly parasitic upon the gametophyte. The lower end of the seta, the *foot*, is thrust a short distance down into the end of the stem of the gametophyte.

Formation of the Spores.—The spore-bearing tissue (Fig. 222, A, *s*) finally gives rise to large, rounded cells, which, because of the enlargement of the capsule, separate from one another. These are the spore mother-cells, from each of which, by division, is formed a tetrad of spores. The first of the two nuclear divisions in the spore mother-cell is the reducing division. Each spore, and every cell of the resulting gametophyte, contains the single number of chromosomes.

Ripening of the Capsule.—When the sporophyte reaches maturity the water supply is cut off from below, and all the cells except the spores die and dry up. The cells of the columella and inner part of the operculum, as well as those within the epidermis, collapse completely, leaving little more than the spores themselves and the firm cell walls of the peristome and the cells connecting the latter with the wall of the capsule. By the breaking down of the thin lateral and transverse walls of the cells that give rise to the peristome, the outer and inner thickened walls of these cells are separated, and form the two rows of membranous teeth that surround the mouth of the capsule. The small cells between the annulus and the margin of the capsule dry up, and by the mechanical action of the annulus the operculum is disconnected and falls off. The ripe capsule consists, therefore, of a thin, dry, urn-like shell with a large cavity containing the spores.

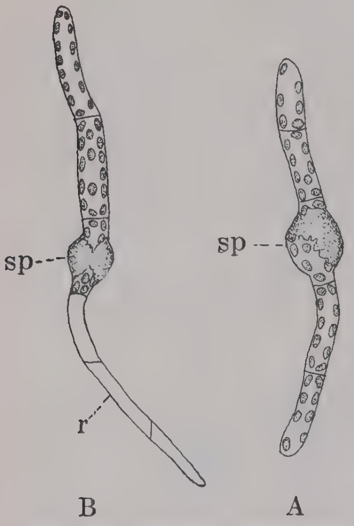

FIG. 224.—*Funaria hygrometrica.* Germinating spores. A, *sp*, spore, both germ tubes containing chloroplasts. B, one tube containing chloroplasts, while the other will function as a rhizoid, *r*.

Germination of the Spore. The wall of the spore consists of two layers, the outer brown *exospore* and the colorless *endospore*. During germination the exospore is ruptured, and the endospore protrudes as a papilla, or the cell may grow in two directions, sending out two germ tubes, one of which may become the first rhizoid (Fig. 224). The growth of the protonema is apical. Under favorable conditions a system of numerous branches is produced resembling an alga. The branches which penetrate the soil have oblique cross walls and undeveloped chloroplasts, thus assuming the character of rhizoids. From the green protonemal filaments above the soil many special branches may arise first as minute green buds, which develop into the well-known leafy moss plants. The complete gametophyte consists of the leafy stems, rhizoids, and protonema. The protonema of the moss may be reasonably regarded as a juvenile form of the gametophyte capable of an unusually prolific vegetative propagation.

In the remarkable moss, Buxbaumia, the gametophyte is a very small flat structure, scarcely visible to the unaided eye, while the sporophyte is large and well developed. At a glance it resembles a bug on a stick (Fig. 223, C).

Classification of Musci

The Musci are grouped in three orders. Sphagnales, Andreaeales, and Bryales. In the following only a few of the genera that contain the more familiar and common mosses are given.

Order 1. Sphagnales
    Sphagnum, Peat Moss, or Bog Moss.
Order 2. Andreaeales
    Andreaea
Order 3. Bryales, True Mosses
    Funaria, Cord Moss
    Catherinia, Pigeon Wheat Moss
    Mnium
    Polytrichum, Hairy Cap Moss
    Climacium, Pine Tree Moss
    Rhodobryum
    Hypnum, Plume, or Feathery Moss
    Buxbaumia
        etc.

SPHAGNALES

All of the Sphagnales are included in the genus Sphagnum. They are commonly found in swampy localities known as bogs, where the partly decayed moss may contribute to the formation of peat. The pale green leaves are borne mainly on the numerous short branches (Fig. 225, A). The leaves do not have a midrib. Each when mature consists of two kinds of cells, large colorless cells, between which are long, narrow cells containing chloroplasts. The large colorless cells are devoid of living contents; their walls usually possess spiral or ring-shaped thickenings on the inside. Round holes are generally present in their walls (Fig. 225, B). Similar colorless cells form the cortex of the stem. There is no central differentiated strand of cells in the stem as in the true moses. The colorless cells of both leaf and stem have a remarkable capacity to take up water, so that the whole plant retains water like a sponge.

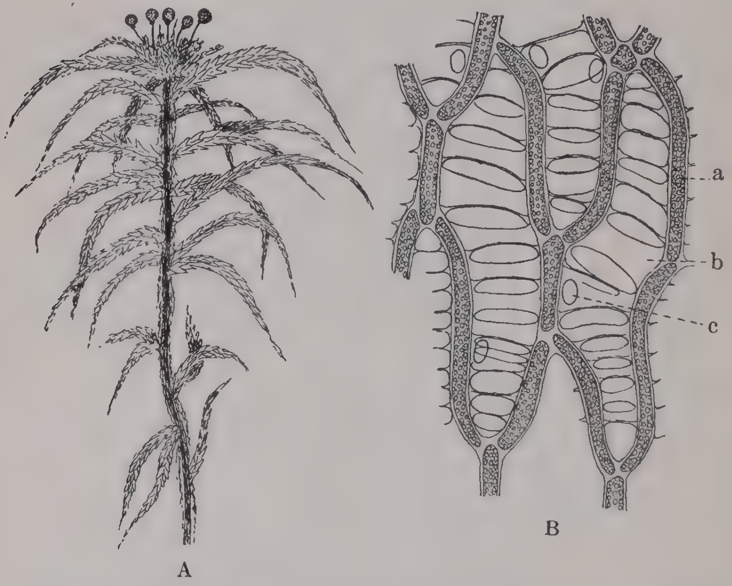

Fig. 225.—Sphagnum. A, Habit of fruiting plant. B, a few cells of leaf. *a*, long, narrow living cells with chloroplasts; *b*, large colorless cells, whose walls have spiral or ring-like inner thickenings; *c*, round hole in cell wall.

The sporophyte has no seta. The slender, naked stalk bearing the sporophyte is the leafless elongation of the stem of the gametophyte, known as the *pseudopodium* (Fig. 226, A, *p*). The pseudopodium is, therefore, *analogous* to the seta of the Bryales but not *homologous* with it. The sporophyte resembles that of Anthoceros in the possession of a columella overarched by the spore-bearing tissue, and a bulbous foot. The capsule has an

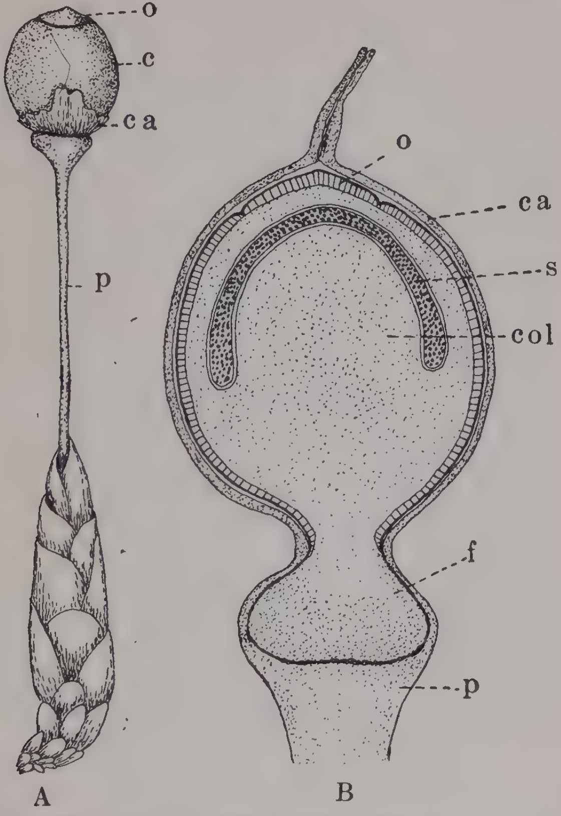

FIG. 226.—Sphagnum. A, short branch bearing sporophyte on the elongated gametophytic stalk, the pseudopodium, *p*. B, median section through sporophyte and upper end of pseudopodium. *o*, operculum; *c*, capsule; *p*, pseudopodium; *ca*, calyptra; *s*, sporogenous tissue; *col*, columella; *f*, foot of sporophyte. (A, from Schimper; B, from Waldner.)

operculum, resembling in that respect the capsule of the Bryales.

The gametophyte of Sphagnum is monoecious in some species and dioecious in others. In the monoecious species the antheridia and archegonia are borne on different branches.

Sphagnum is used as a packing material and for many other purposes. During the world war certain species were used along with other materials in making surgical dressings.

The protonema is thalloid, resembling a small liverwort of simple structure.

ANDREAEALES

This order includes a group of small mosses intermediate in character between the Sphagnales and the Bryales. The capsule opens by longitudinal slits. The spore-bearing tissue extends over the columella somewhat as in Sphagnum.

BRYALES

This order contains the vast majority of mosses. The numerous species are grouped under several families and in many genera. A few genera, to which some of the more commonly known mosses belong, are listed in a preceding paragraph.

CHAPTER XVI

PTERIDOPHYTA

The most striking characteristic distinguishing the Pteridophyta from the liverworts and mosses is seen in the large, long-lived, and independent sporophyte, the plant recognized as the fern, which is differentiated into root, stem, and leaf, each of these organs possessing a well developed vascular system. Among the common ferns the gametophyte, known as the *prothallium*, is usually a relatively small, heart-shaped plant of simple structure, usually very much smaller then the gametophyte of the liverwort or moss. As a rule, the prothallium produces but one sporophyte, although several sporophytes may be made to develop on a single prothallium under experimental conditions in the laboratory. The prothallium contributes to the nourishment of the sporophyte until the latter has become self-sustaining in the production of one or more leaves and one or more roots. Soon after this condition has been attained by the sporophyte, the gametophyte becomes exhausted and dies.

LIFE HISTORY OF A FERN

As an illustration of the life history of the fern, one of the Polypodiaceae will serve as a type.

The Sporangium.—In ferns of this family the sporangia are borne either on foliage leaves or on leaves completely modified into purely spore-bearing structures.

The sporangia are aggregated in clusters, *sori*, and each sorus is usually covered by an outgrowth of the leaf, and *indusium* (Fig. 227, A, B). In the Maiden

Hair fern (Adiantum) the sporangia are covered by the folded-over margin of the leaflet, which constitutes a *false indusium* (Fig. 227, C, *a*). Each sporangium consists of a flattened body, or capsule, borne on a slender stalk (Fig. 228). The wall of the sporangium consists of a single layer of cells. Around the edge is a row of modified cells, the ring, or *annulus*, which, by a purely mechanical action, opens the sporangium. The place of dehiscence, or opening, is indicated at one side by two narrow cells that form the *stomium* (*st*).

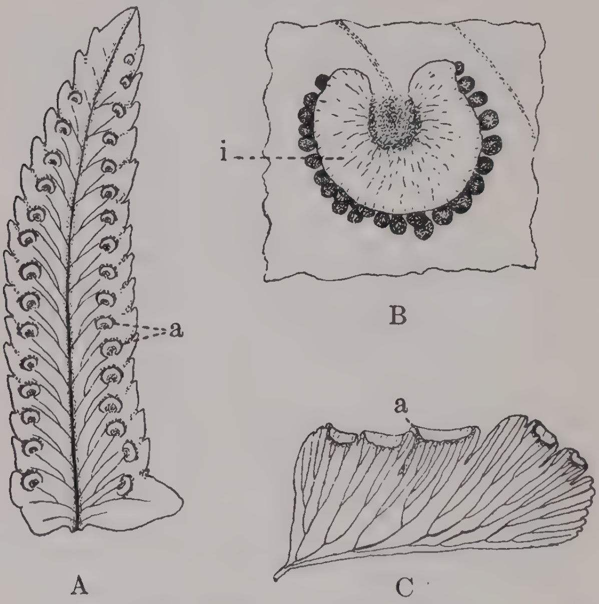

Fig. 227.—Spore-bearing leaflets of common ferns. A, B, Boston fern (*Nephrolepis exaltata*). C, Maiden-Hair Fern (*Adiantum pedatum*). A, pinna with sori, *a*. B, enlarged sorus with indusium, *i*. C, pinna with sori, *a*, covered by the folded margin of the leaflet, a *false indusium*.

Opening of the Sporangium.—Dry weather is necessary for the opening of the sporangium. As will be seen in Fig. 228, the cells of the annulus have thick radial and inner walls, while the outer walls are thin.

The thickened inner and radial walls form U-shaped curves. When the mature sporangium dries, the annulus straightens out slowly and breaks the capsule open

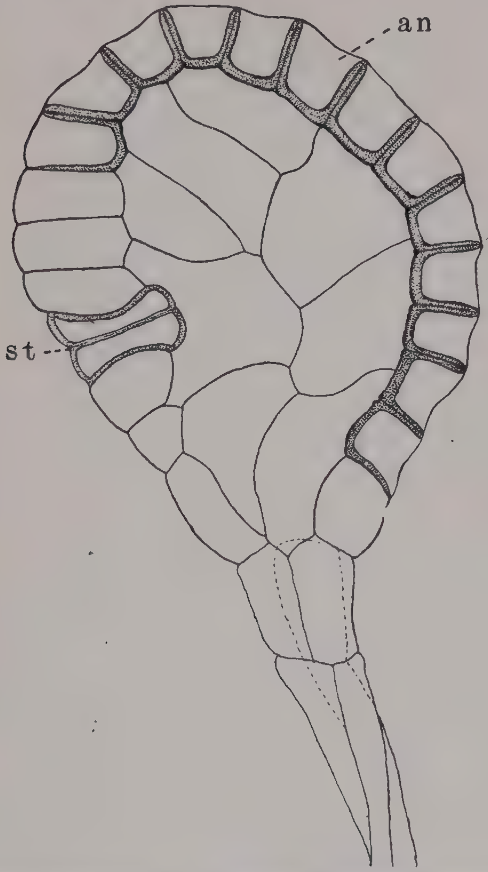

FIG. 228.—Mature sporangium of *Nephrolepis exaltata*, in surface view; *an*, annulus; *st*, stomium, or place of opening.

transversely at the stomium. The straightening process continues to such a degree that the annulus bends back upon itself, or turns inside out (Fig. 229, A), when, with a sudden snap or jerk, it returns to its original position (Fig. 229, B). This catapult-like action tosses the spores out into the air. The process may be repeated, and in this manner the spores may be expelled.

The annulus is everted when the parallel sides of the U-shaped cells come close together, bending the thin outer walls, as shown in Fig. 229, C. The shape of the cells of the annulus before the sporangium opened is shown at D.

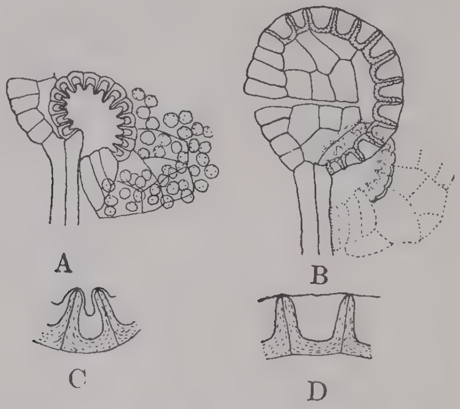

Fig. 229.—A, sporangium with annulus turned inside out, or everted. B, similar sporangium after recovery by a sudden snap or jerk. C, condition of cells of the annulus when everted. D, cells of annulus before sporangium opens. (From F. O. Bower's "Botany of the Living Plant." By permission of the Macmillan & Company, Ltd., Publishers.)

The Gametophyte, or Prothallium.—For a study of the gametophyte we shall select the Ostrich Fern (*Matteuccia nodulosa*). The spore has a wall consisting of three layers, namely, the outer, brown *perinium*, the middle layer, *exine*, or *exospore*, and the inner cellulose layer, *endospore*, or *intine*. The exospore and endospore are colorless.

As the spore germinates, the perinium bursts and often falls away. The exospore is also ruptured, but the endospore remains as the wall of the growing cell (Fig. 230, A, B). A papilla is now sent out through the rupture in the exospore. The cell divides, cutting off the papilla as a small cell, which grows into the first rhizoid (Fig. 230, C). The larger cell now begins development into the body of the gametophyte. By rapid growth and division, a short row of cells is soon formed (D). If the spores are grown on water, a more filamentous and irregular structure will result.

At a very early stage in development, an oblique division will occur in one of the distal cells, thus establishing a V-shaped apical cell (*a*). This apical cell, by further successive divisions, cuts off cells alternately from the two sides. Such an apical cell is said to possess two "cutting faces." The subsequent growth and division of the cells thus formed from the apical cell give rise to two symmetrical wings, or lobes, of the prothallium, and the result is the conventional heart-shaped plant (Fig. 231, A, and 232).

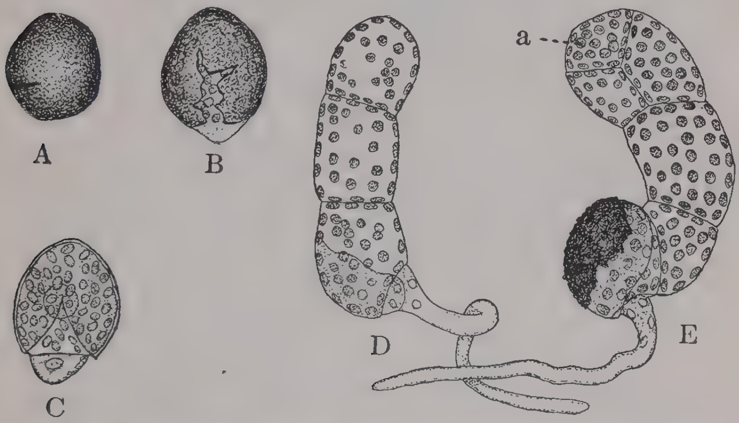

Fig. 230.—*Matteuccia nodulosa.* Germinating spores and early stages in the development of the prothallium. A, spore before rupture of wall. B, bursting of perinium. C, the perinium has fallen away, the exospore is ruptured, and the papilla to form the first rhizoid is cut off. D, the spore has given rise to a 3-celled prothallium with one rhizoid. E, prothallium in which the apical cell, *a*, has been established.

At a later stage in development than that shown in Fig. 231, A, the V-shaped apical cell divides transversely into two cells, a larger, outer, rectangular cell, and an

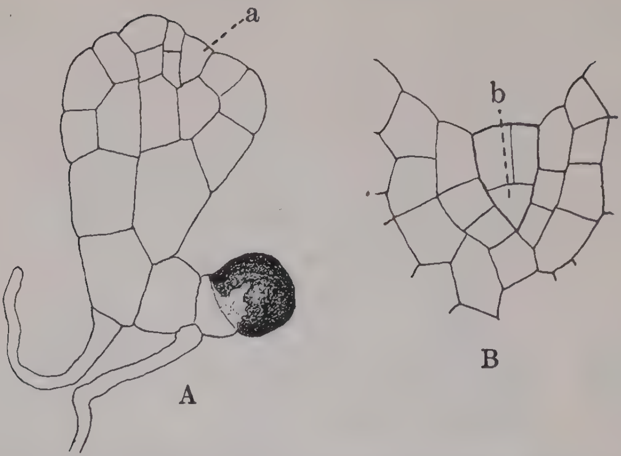

FIG. 231.—*Matteuccia nodulosa.* A, young prothallium which has become heart-shaped; *a*, apical cell. B, apical region in which the V-shaped cell has given rise to rectangular apical cells with three cutting faces; *b*, the cell cut off from the pointed end of the V-shaped cell.

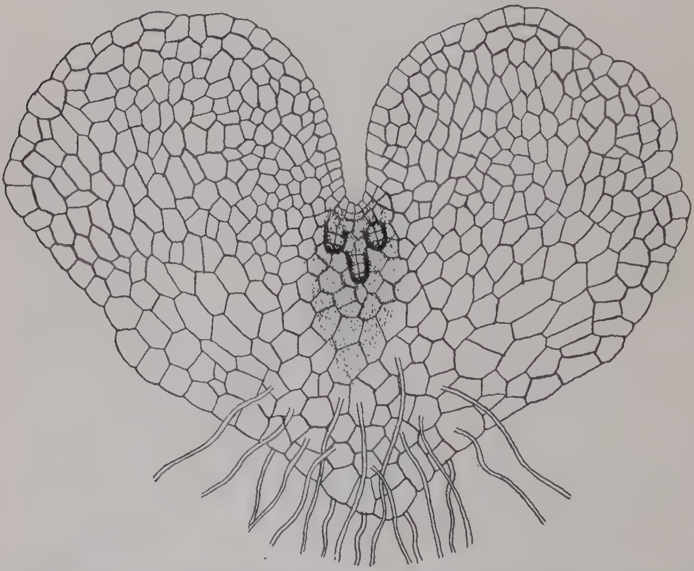

FIG. 232.—*Matteuccia nodulosa.* A female prothallium bearing three archegonia near the growing edge, or apical sinus.

inner cell triangular in surface view (Fig. 231, B). The outer cell now has three cutting faces. It can divide by cutting off cells from both the right and left sides, and from the inner side or end. The outer, or anterior side of this cell is rounded in a dorsiventral direction. By longitudinal divisions this cell may give rise to several apical cells, the number depending on the width of the apical sinus (Fig. 232). The cells cut off from the inner ends of the apical cells divide in three planes, thus giving rise to the more massive midrib, or archegonial cushion. The wings of the prothallium remain one cell in thickness.

From the margin and under surface of the posterior part of the prothallium, numerous one-celled rhizoids develop. As soon as the midrib is established, the prothallium is large enough to bear archegonia.

Sex Organs.—In strictly monoecious prothallia, both kinds of sex organs are borne on the same plant, the antheridia on the older posterior part, and the archegonia just back of the growing point.

Antheridium.—In many ferns it frequently happens, especially under cultural conditions, that certain prothallia will begin to develop antheridia while quite small, and these organs may be produced in such large numbers that the plants never attain a larger size (Fig. 234, A, and Fig. 233). Other prothallia will, on the contrary, produce few or no antheridia, but continue to grow to a larger size, when both sex organs, or only archegonia, will be developed. When the spores are sown thickly on earth, large numbers of the plants will remain small, bearing only antheridia. In *Matteuccia nodulosa* and *Onoclea sensibilis,* there is a tendency toward dioecism under the most favorable cultural conditions, but all prothallia are potentially bisexual.

The antheridia are borne at the margins and on both surfaces. They are usually hemispherical or thimble-shaped. The wall of the antheridium consists of three cells, a basal, funnel-shaped cell, a middle, ring-shaped cell, and a lid cell (Fig. 234, *b*, *r*, *l*). These three enclose a mass of cells, the sperm initial cells, which will give rise to the sperms.

The mature sperm is a spiral-shaped body bearing many cilia (Fig. 234, E). The larger, posterior part of the sperm is derived from the nucleus, while the anterior portion comes from the cytoplasm. At the edge of the cytoplasmic portion is a delicate thread, the *blepharoplast,* which bears the numerous cilia. The sperm is, therefore, merely a naked cell so transformed as to be capable of locomotion in water.

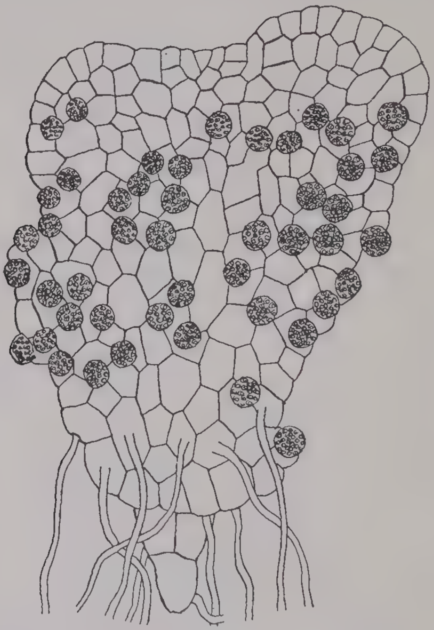

Fig. 233.—Male prothallium of *Matteuccia nodulosa*, bearing many antheridia.

When the antheridium is mature, the application of water will lead to its opening by the bursting, or separation, of its lid cell (Fig. 234, D). The sperms are expelled by the pressure exerted against them by the turgid basal and ring cells. Free from the antheridium, each sperm escapes almost immediately from the delicate, colorless membrane surrounding it and swims away.

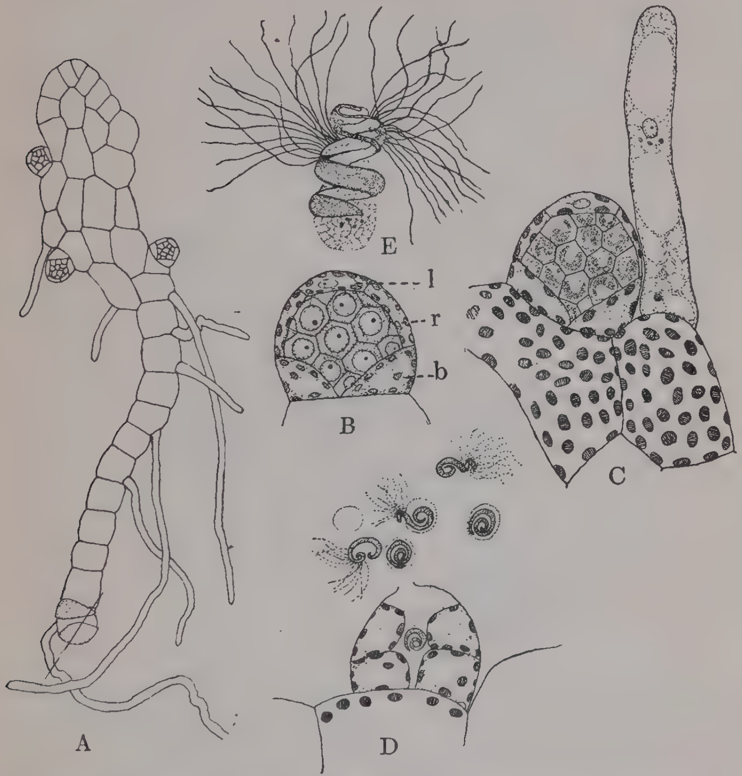

Fig. 234.—*Matteuccianodulosa.* Antheridia and sperms. A, small prothallium bearing three antheridia. B, antheridium more highly magnified, containing a mass of sperm-bearing cells; *l*, lid cell; *r*, ring cell; *b*, basal cell. C, two marginal cells and one young rhizoid of prothallium with one antheridium, in which sperms are about half grown. D, antheridium from which sperms are escaping. E, a sperm, very highly magnified.

The Archegonium.—In our ordinary ferns (Polypodiaceae) the archegonia are borne on the under side of the prothallium just back of the growing point, although a few may be developed on the dorsal side as well (Fig. 235).

The mature archegonium is flask shaped, but smaller and more simple in structure than that of the moss. Its venter is embedded in the tissue of the midrib, only the neck protruding beyond the surface. The fully formed

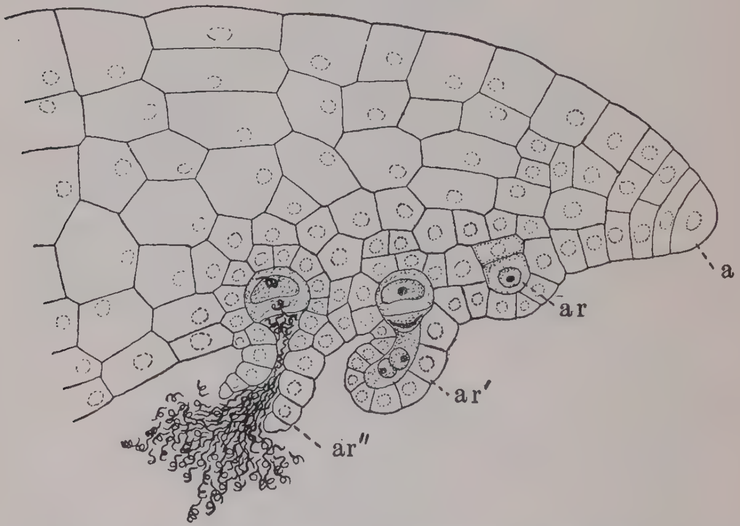

FIG. 235.—*Matteuccia nodulosa.* Longitudinal section through the growing point of the prothallium; *a*, apical cell; *ar*, young archegonium; *ar′*, fully developed archegonium; *ar″*, open archegonium in which fecundation is taking place, one sperm nucleus being inside the egg nucleus.

archegonium consists of an axial row of cells surrounded by a single layer of cells. The lowest, or innermost, of the axial row of cells, which lies in the venter, is the egg. Above it is the small ventral canal-cell, and extending up into the neck is the neck canal-cell (Fig. 235, *ar′*). The neck is generally curved backward or to one side. The wall of the neck consists of four rows of cells. The egg and ventral canal-cell are sisters. In the neck canal cell are almost invariably found two nuclei in Onoclea, Matteuccia, and other Polypodiaceae. The ventral canal-cell and neck canal-cell undergo mucilaginous degeneration as the archegonium matures.

Fecundation.—Application of water to the ripe archegonium causes it to open. The end cells of the neck separate, and the mucilaginous contents begin to diffuse out into the water. This substance exerts a positive chemotactic stimulus on the sperms, so that if any approach the open neck, they will enter and pass down to the egg. The entire sperm enters the cytoplasm of the egg, where its cytoplasmic portion remains, while the nucleus of the sperm passes into the nucleus of the egg (Fig. 235, *ar″*). Within the nucleus of the egg that of the sperm gradually breaks up into smaller particles, so that finally the particles of the two nuclei can no longer be distinguished from one another. Fecundation is then complete.

Development of the Embryo Sporophyte.—Soon after fecundation the venter of the archegonium closes, whereas the neck dies and turns brown. A cellulose wall is formed about the zygote, which begins growth and division immediately. The first division of the zygote is parallel with the long axis of the archegonium. The two resulting hemispherical cells divide simultaneously in a plane at right angles to the first division wall. The embryo now consists of four cells, or quadrants, each of which is the starting point of one of the four definite regions of the developing embryo, namely, *stem*, *leaf*, *root*, and *foot*. The upper anterior quadrant gives rise to the stem; the lower anterior develops into the first leaf; the lower posterior produces the first root; and the upper posterior becomes the foot. The subsequent cell divisions in each quarter are very regular at first, but the details will not be given here. As a result, however, we have a many-celled, globular embryo, in which the four original parts may be readily recognized in longitudinal vertical section, as shown in Fig. 236.

The region of the stem reveals the apical cell (*st*) of that organ; the initial cells of the first leaf (*l*) and of the root (*rt*) are also plainly shown.

As the embryo grows larger, these four regions develop at different rates, and the globular embryo soon takes the shape of a shoe (Fig. 237). At this stage, however, it is still enclosed in the calyptra. From this figure it is clear that the foot (*ft*) is a broad region whose cells merge gradually into those of the gametophyte. The leaf, ending in its apical cell (*l*) has elongated appreciably. The apical cell of the root (*rt*) has given rise to the root cap. The stem (*st*) develops at first more slowly than the other three regions.

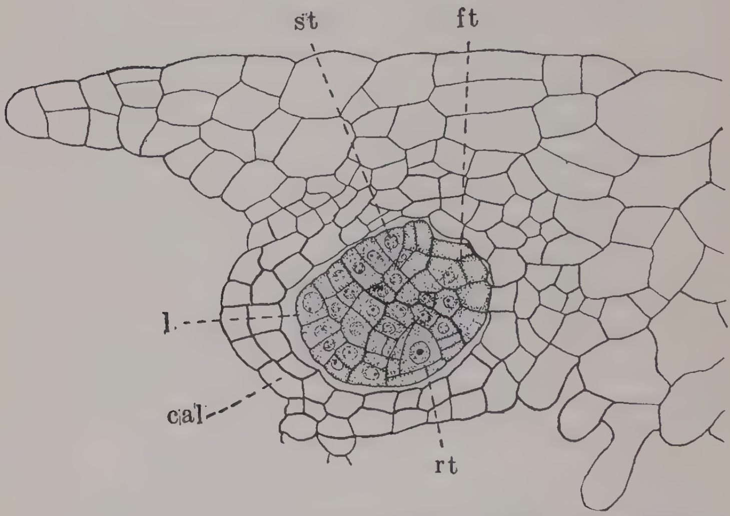

Fig. 236.—*Matteuccia nodulosa.* Longitudinal section of a gametophyte containing embryo sporophyte in which the four regions, leaf (*l*), stem (*st*), root (*rt*), and foot (*ft*) are clearly differentiated; *cal*, calyptra.

With further growth, leaf and root develop rapidly, soon breaking through the calyptra, which, as in the bryophytes, is derived from the venter of the archegonium. The leaf curves upward into the air through the notch of the prothallium, while the root strikes obliquely downward into the soil. The young sporophyte attached to the gametophyte is shown in Fig. 238, A, B. A is a view from above, while B is the same specimen as seen from below. The stem (*st*) is concealed behind the base of the leaf, and the foot is embedded in the gametophyte, posterior to the very short stem. In Fig. 239, A, we have a side view of the young fern dissected from the prothallium. The relation to one another of stem (*st*), leaf (*l*), root (*rt*), and foot (*ft*) is evident.

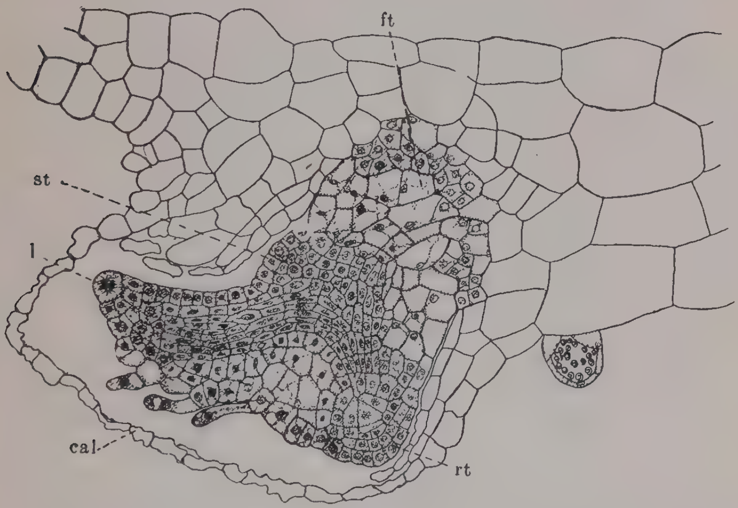

Fig. 237.—*Dryopteris mollis.* Longitudinal section of gametophyte with a larger embryo sporophyte. The first leaf, *l*, is about to break through the calyptra, *cal;* the root, *rt*, is provided with a root cap; the large cells of the foot, *ft*, merge insensibly with the neighboring meristematic cells of the gametophyte, while the stem, *st*, is relatively small.

Running through the center of leaf and root is the procambial strand (indicated by the dotted line) of elongated cells, the beginning of the vascular system of the young fern. The procambial strand differentiated in the stem connects with this main strand of leaf and root. The stem is at first so small in comparison with leaf and root that the vascular system can be said to originate in leaf and root.

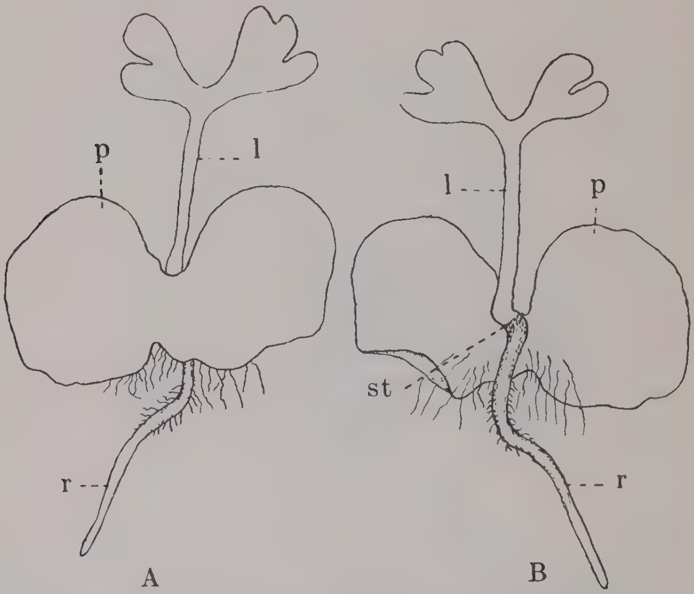

Fig. 238.—*Matteuccia nodulosa.* A, upper, and B, lower view of the same gametophyte with sporophyte attached; *l*, first leaf; *r*, first root; *p*, prothallium; *st*, stem.

As the young fern continues its growth, additional leaves and roots appear. The first leaf, sometimes referred to as the *cotyledon*, never attains a large size. Each subsequent leaf, however, becomes larger than its predecessor, and the process continues until the adult size is attained. A similar course of development is followed in the roots. In the young fern shown in Fig. 239, B, the second root (r^2) has grown out of the side of the short stem, and the second leaf (l^2) is emerging from the end of stem, which, in this view, is concealed by the base of the first leaf.

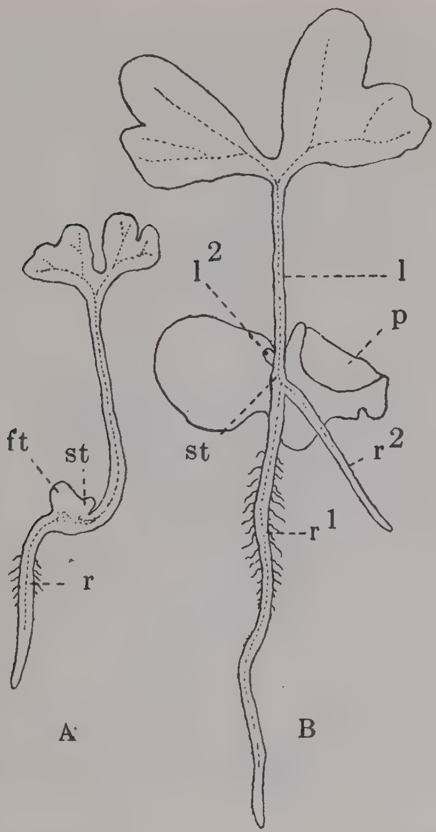

FIG. 239.—*Matteuccia nodulosa.* A, side view of young fern from which the gametophyte has been detached; primary vascular system indicated by a dotted line; *l*, leaf; *r*, root; *st*, stem; *ft*, foot. B, an older plant, attached to prothallium, showing second root, r^2, and beginning of second leaf, l^2; *p*, prothallium; *l*, first leaf; r^1, first root.

The Mature Sporophyte.—As stated in a preceding paragraph, the mature fern consists of stem (rhizome, or rootstock), leaves, and roots. In such ferns as Adiantum and Onoclea the stem grows horizontally near the surface of the ground. It is dark brown in color, being covered by a coat of small brown scales. It branches monopodially, and new leaves arise annually from the growing end or ends. The older parts gradually die and decay (Fig. 240).

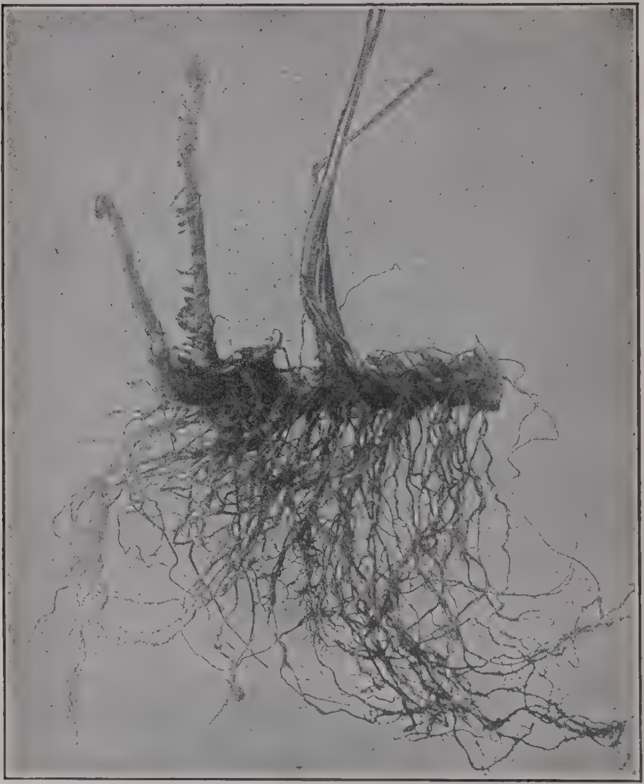

FIG. 240.—*Adiantum pedatum.* Part of sporophyte after growth has begun in the spring; two young leaves are "coming up."

The Stem.—In typical ferns growth of the stem proceeds from a tetrahedral apical cell. In unbranched stems the apical cell is a continuation of that originating in the stem quadrant of the embryo.

The Leaf.—When the stem is horizontal, the leaves arise mainly from the dorsal surface. Where the stem is upright, the leaves usually form a crown encircling the growing end, as in the evergreen fern *Dryopteris marginalis* (L.) A. Gray (*Aspidium marginale* (L.) Sw.). In the vast majority of ferns the young leaf is coiled up in the bud like a watch spring. The veins may be free or form a network of anastomosing branches. The structure of the leaf blade, in regard to the arrangement of tissues, is similar to that in the higher plants.

The Root.—The first root developed from the embryo is small and of short duration, while those following are larger and may continue to grow during the life of that part of the stem bearing them. In most of our ordinary ferns the roots are much branched and arise near the base of the leaves or from the base of the leaves. In tree ferns the roots may form a thick, matted mass covering the stem.

Development of Sporangium and Spores.—In our ordinary ferns (Polypodiaceae) the sporangium originates from a single epidermal cell. Several early stages in the development are shown in Fig. 241, A to F. In the young sporangium (F, *s*) is differentiated a central mass of cells that will give rise to the spores. This central mass is surrounded by two layers of tabular cells constituting the tapetum, or nourishing cells (*t*). The wall of the sporangium is one cell thick, the row around the edge developing into the annulus. As the sporangium attains the mature size, the spore mother-cells round off and separate, the tapetal cells being changed into a liquid by digestion. Each spore mother-cell produces a tetrad of four spores, as a result of two successive divisions of the nucleus and final cell divisions. The first nuclear division in the spore mother-cell is a reducing division. The spore possesses, therefore, the single number of chromosomes.

Vegetative Propagation of the Gametophyte.—If the life of fern prothallia be prolonged, vegetative propagation may be accomplished chiefly by the production of numerous lobes or proliferations, which are separated by the death of older parts. In laboratory cultures, prothallia of certain ferns (Matteucia, Osmunda) may branch dichotomously, and the branches may ultimately be separated by the dying away of older parts as in the liverworts.

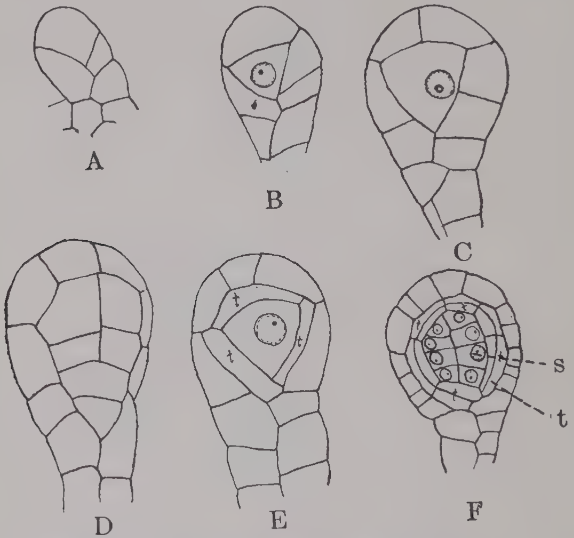

Fig. 241.—Stages in the development of the sporangium of *Polypodium falcatum*. A to F, successive stages in development from a single cell. D and E, surface and sectional views, respectively, of the same stage in development; *t*, tapetum; *s*, spore-bearing cells. (From Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers.)

Vegetative Propagation of the Sporophyte.—A much greater variety of vegetative propagation is presented by the sporophyte. Here one of the most conspicuous kinds is the production of modified stems in the form of stolons, which take root and send up leaves. This is common in varieties of the Boston fern (*Nephrolepis* *exaltata*). In certain ferns (*Cystopteris bulbifera* (L) Bernh.) small bulbils are developed on the leaves. These fall off and may give rise to new plants. Another striking method is found in the Walking Fern (*Camptosorus rhizophyllus*), in which the tips of the leaves take root and produce new plants. New plants may arise also from the fleshy roots of ferns, as in Ophioglossum.

Apogamy and Apospory.—Apogamy refers to the condition in which a sporophyte arises as a vegetative outgrowth from the gametophyte, and, of course, without the functioning of gametes. Of a considerable number of ferns in which apogamy is known to occur may be cited two cliff brakes, *Pellaea atropurpurea* and *Pellaea glabella*, which grow on limestone ledges and escarpments. On the prothallia of these species antheridia with normal sperms are regularly developed, but no archegonia. The sporophyte arises as an outgrowth from the anterior part of the archegonial cushion (midrib).

On the other hand, the term, *apospory*, is applied to the origin of gametophytes from the sporophyte without the functioning of spores. In certain ferns, which are aposporous, if the leaf blades be fastened against the surface of the soil, prothallia bearing sex organs and functional gametes will develop, generally from spots on the leaf which would normally produce sporangia.

Classification of the Pteridophytes

The Pteridophyta may be divided into three great classes: *Filicales*, ferns and their allies; *Equisetales*, horsetails and scouring rushes; and *Lycopodiales*, club mosses.

Although gametophyte and sporophyte in these great classes may differ widely in habit, structure, and adaptation to environment, the life history, when traced from spore to spore, is fundamentally the same as that given in the preceding pages for a commonly known fern.

The following classification is intended as an abbreviated outline:

CLASS 1. FILICALES. Ferns and fern-like plants

SUB-CLASS 1. Eusporangiate ferns. Sporangia without an annulus, opening vertically in two valves. In development the whole sporangium is not readily traced back to a single epidermal cell. All are homosporous.

Family: Ophioglossaceae. Leaves not rolled up in the bud like a watch spring.
Ophioglossum, Adder's Tongue Fern.
Botrychium, Moonwort; Rattlesnake Fern.

Family: Marattiaceae. Sporangia without an annulus. All Tropical. Marattia; Angiopteris.

SUB-CLASS 2. Leptosporangiate ferns (Filices). Sporangium arising from a single epidermal cell.

(*a*) Homosporous. One kind of spore.

Family: Osmundaceae. Sporangia with rudimentary annulus; opening vertically.
Osmunda, Interrupted Fern, Cinnamon Fern, Royal Fern.

Family: Polypodiaceae. Sporangia with complete annulus.
Matteuccia, Ostrich Fern.
Onoclea, Grape Fern; Sensitive Fern.
Adiantum, Maidenhair Fern.
Pteris (Pteridium), Brake Fern.
Dryopteris, Shield Fern; Christmas Fern.
Asplenium, Spleenwort.
Polypodium, Polypody.
Camptosorus, Walking Fern.

(*b*) Heterosporous. Spores of two kinds, microspores and megaspores, producing respectively male and female gametophytes.

Family: Marsiliaceae, Pepperworts.
Marsilia; Pilularia.
Family: Salviniaceae. Azolla; Salvinia.

CLASS 2. EQUISETALES. Horsetails

Equisetum.

CLASS 3. LYCOPODIALES. Club Mosses

Family: Lycopodiaceae.
Lycopodium.
Family: Selaginellaceae.
Selaginella.
Family: Isoetaceae.
Isoetes. Quillwort.

Ophioglossaceae.—This family is represented in our flora by two genera, Ophioglossum and Botrychium. Species of both genera are rapidly approaching extinction, owing to the disappearance of the native woodlands.

Ophioglossum is a small fern with a short, upright underground stem, bearing fleshy roots, and sending up each year a single leaf. At the side of the base of the naked leaf stalk is the bud (Fig. 242, A, *b*). In spore-bearing specimens the leaf has a vegetative and a spore-bearing segment (Fig. 242, A, *s*). The sporangia are completely embedded, and open by a transverse slit (B). The sporophyte is propagated vegetatively from the fleshy roots.

The gametophyte in both Ophioglossum and Botrychium is a small, dark brown, tuber-like, subterranean body, irregular in form, and about one to one and a half centimeters or more in length (Fig. 244, A, B, *g*). It is destitute of chlorophyll. The cells of the ventral part

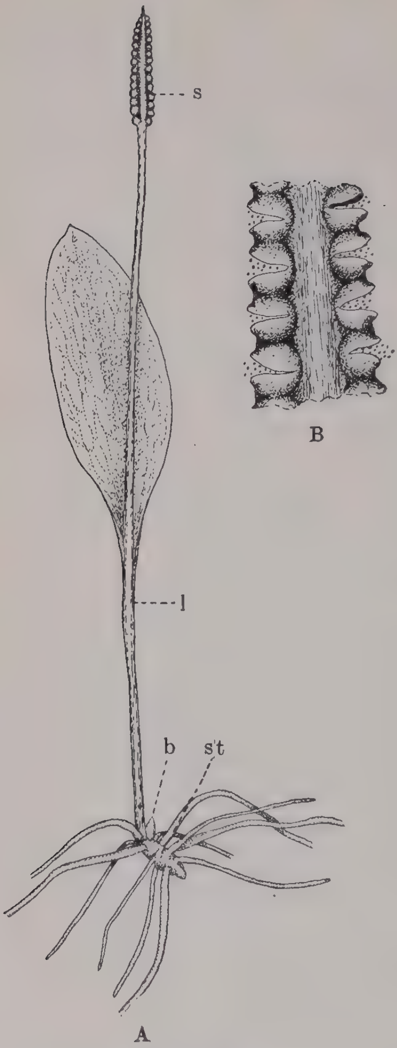

Fig. 242.

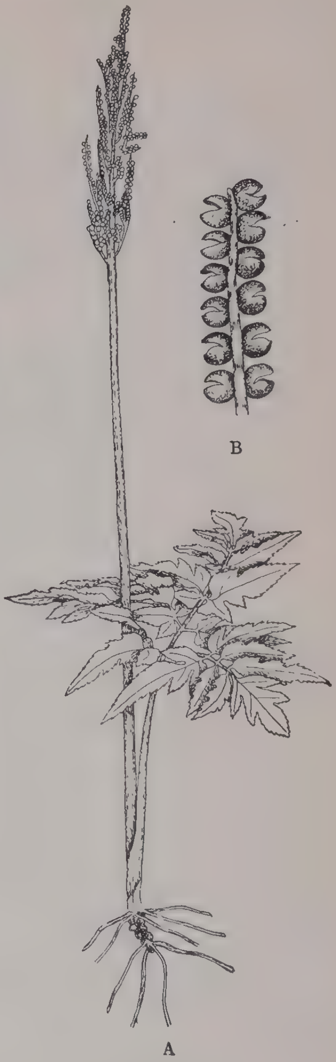

Fig. 243.

Fig. 242.—*Ophioglossum vulgatum.* A, habit of plant, slightly reduced; *l*, leaf; *s*, spore-bearing segment of leaf; *st*, stem; *b*, bud. B, portion of spore-bearing segment of leaf, showing manner of opening of the embedded sporangia.

Fig. 243.—*Botrychium obliquum.* A, whole plant (sporophyte). B, a pinna with open sporangia (enlarged).

contain an endophytic fungus, which doubtless assists the plant in securing nourishment from the soil. The relation between the gametophyte and the fungus is probably one of mutual symbiosis. The sex organs are

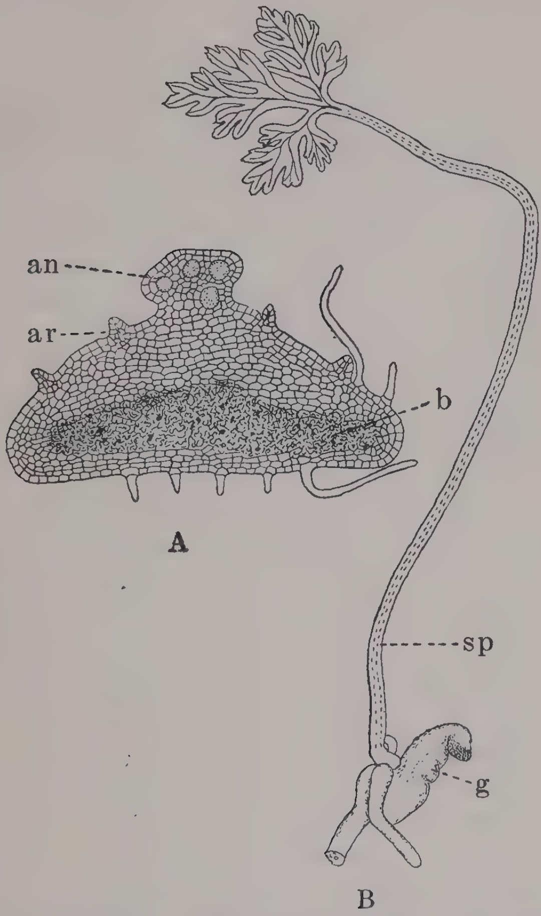

FIG. 244.—*Botrychium virginianum*. A, transverse section of gametophyte; *an*, antheridial ridge with imbedded antheridia; *ar*, archegonia; *b*, region containing endophytic fungus. B, gametophyte, *g*, with young sporophyte, *sp*, attached. (A, from Jeffrey; B, from Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers.)

developed on the dorsal side, the antheridia being confined largely to the dorsal ridge, and the archegonia to the slopes (Fig. 244, A). The antheridia are deep-seated.

In Botrychium the leaf requires three or more years to reach maturity. The base of the leaf forms a sheath which completely encloses the apex of the stem and the bud. In spore-bearing specimens the leaf has also two segments, both much branched, the spore-bearing and the foliage (Fig. 243, A, B). In Fig. 244, B, is shown a young sporophyte still attached to its gametophyte (*g*).

Marattiaceae.—The Marattiaceae include a small number of tropical species, which, in general appearance, resemble ordinary ferns. In temperate climates they are cultivated in large conservatories along with large tree ferns (Cyatheaceae) and other exotics. In Marattia and Angiopteris the stem is a thick, stocky, tuber-like structure, which may attain a diameter of half a meter, with a crown of leaves that may attain a length of four or more meters. The leaves are circinate in the bud.

The sporangia, which are borne on the foliage leaves, are united into masses known as *synangia*, in which the individual sporangia are not always clearly recognized. The sporangia do not have a ring, but open by a longitudinal slit.

The gametophyte is a fleshy, green thallus, resembling a small liverwort in appearance. It is monoecious, both sex organs being borne on the under side. Endophytic fungi are present in some species.

Osmundaceae.—The Osmundaceae are large, handsome ferns often found in wet or marshy places, where they form large tussock-like clumps. The tall, graceful leaves, once or twice pinnate, may attain a length of one and one-half meters. When young the leaves are clothed with a loose, light-colored wool. In *Osmunda claytoniana* L. the sporangia are restricted to two to five pinnae near the middle of certain of the leaves. These pinnae are completely transformed into spore-bearing structures. In *Osmunda cinnamomea* L., commonly known as the Cinnamon Fern, the leaves are of two kinds, foliage and spore-bearing. The spore-bearing leaves appear first in the season, but they soon wither and disappear after the spores are shed. The rusty-brown wool covering the leaves when young, together with the brown, shriveled sporangia, give these structures a decided cinnamon color. The foliage leaves are larger, often attaining a length of one and one-half meters. *Osmunda regalis* L. is cosmopolitan in distribution. The spore-bearing leaflets are confined to the summit of the leaf, where they form a sort of racemose panicle. This species is often referred to as the "Flowering Fern." *O. claytoniana* is easily cultivated. The species of Osmunda are in danger of becoming extinct in Indiana.

Polypodiaceae.—These include the vast majority of the common ferns now in existence. They often occur in great numbers, and are widely distributed over the earth.

Marsiliaceae and Salviniaceae.—These are either floating aquatics (Salviniaceae) or they grow in localities that are wet or swampy, at least for a part of the year. The sporophytes produce two kinds of spores: small microspores, which give rise only to male gametophytes, and relatively large megaspores which produce female gametophytes.

Marsilia will serve to illustrate the life history. The sporophyte consists of a slender, creeping, branched stem consisting of nodes and internodes. From the nodes arise numerous roots and leaves, each of the latter having four small triangular leaflets, which give the plant the appearance of a tuft of four-leaved clover (Fig. 245). The spores are borne on modified leaf segments termed *sporocarps*. The sporocarp, which has a hard shell, resembles a small, flat bean (*sp*). Within the sporocarp both microsporangia and megasporangia are developed in clusters. Only one megaspore is fully developed in a megasporangium, while the microspor-

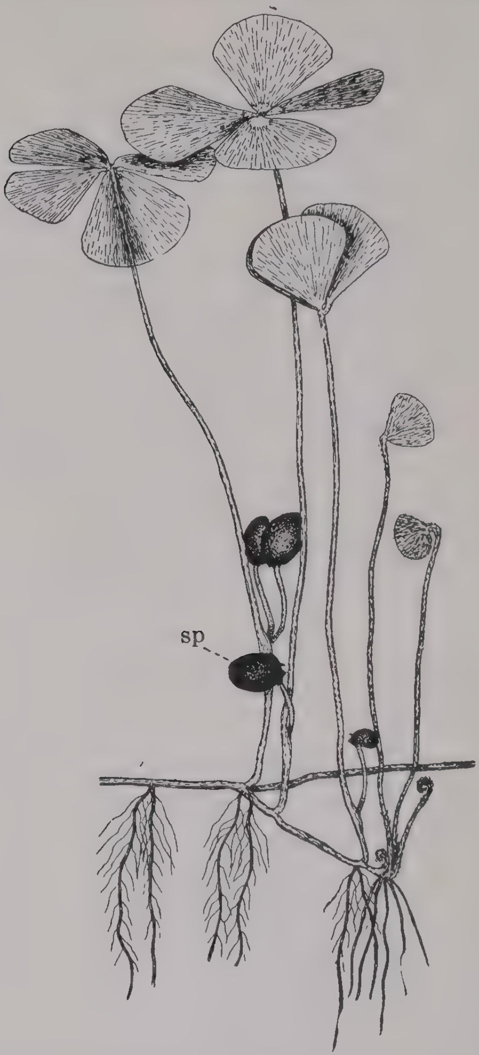

FIG. 245.—*Marsilia quadrifolia.* Habit of sporophyte; *sp*, sporocarp.

angium produces a large number of microspores. In volume a megaspore is several hundred times as large as a microspore. The difference in size is shown in Fig. 247, A and B, which were drawn to the same scale.

A short time after the sporocarps are placed in water, especially if a small opening has been made in the shell, the entire contents will escape in the form of a colorless, gelatinous cord bearing two rows of sori, each sorus containing both kinds of spores (Fig. 246, B).

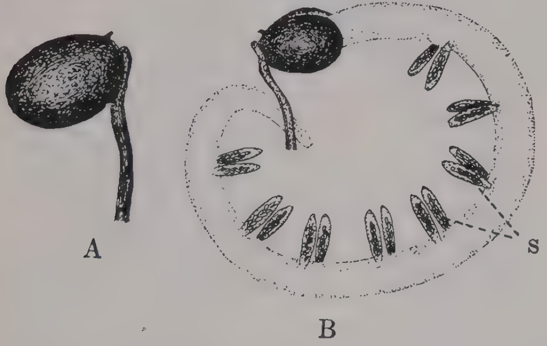

Fig. 246.—*Marsilia quadrifolia.* A, sporocarp (enlarged). B, germinating sporocarp, showing gelatinous cord, to which sori, *s*, are attached.

With the exception of the spores, the entire cellular structure within the hard wall is converted into the colorless jelly.

The Microgametophyte.—The microspore has a wall of three layers, the outer layer being very thick and composed of small, prismatic rods. The microgametophyte is very small, merely filling the cavity of the spore. It develops with great rapidity, reaching maturity in fifteen or twenty hours after the spore begins to germinate. It consists of two vegetative cells (Fig. 247, D, *x*, *y*) and an antheridium bearing two masses of sperms. The two masses of spermogenous cells have been regarded as representing two antheridia. The sperms are shaped like a corkscrew, having a dozen or more turns, and bearing many cilia (Fig. 247, E).

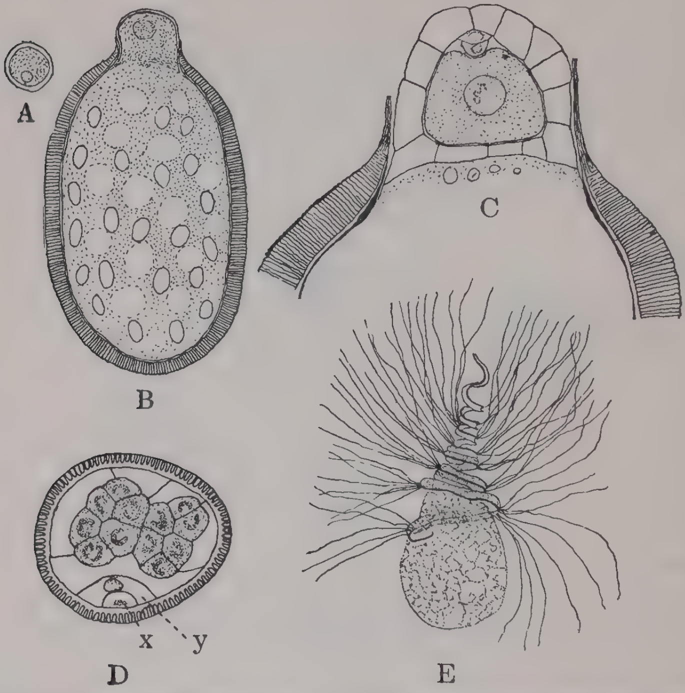

FIG. 247.—*Marsilia quadrifolia.* A, B, microspore and megaspore, drawn to the same scale. C, upper end of megaspore with the megagametophyte, consisting of an archegonium. D, microspore, containing microgametophyte (× 400); *x*, *y*, vegetative prothallial cells; the sperm-bearing cells are shaded. E, a sperm, highly magnified. (C, D, from Campbell's "Mosses and Ferns." By permission of the Macmillan Company, Publishers.)

The Megagametophyte.—The megaspore is an ellipsoidal cell, about .4 by .7 mm. in diameter, ivory-white in color, and provided with a very thick wall. Like that of the microspore, the wall consists of three layers, the outer being thicker and prismatic in structure (Fig. 247, B). At one end of the spore there is a rounded protuberance, in which lie the nucleus and the bulk of the cytoplasm. The thick prismatic layer of the cell wall does not cover this protuberance. The cavity of the spore is rich in food material, composed chiefly of starch and protein. The megagametophyte, like the microgametophyte, is reduced to its lowest terms, consisting merely of an archegonium with a very short neck (C).

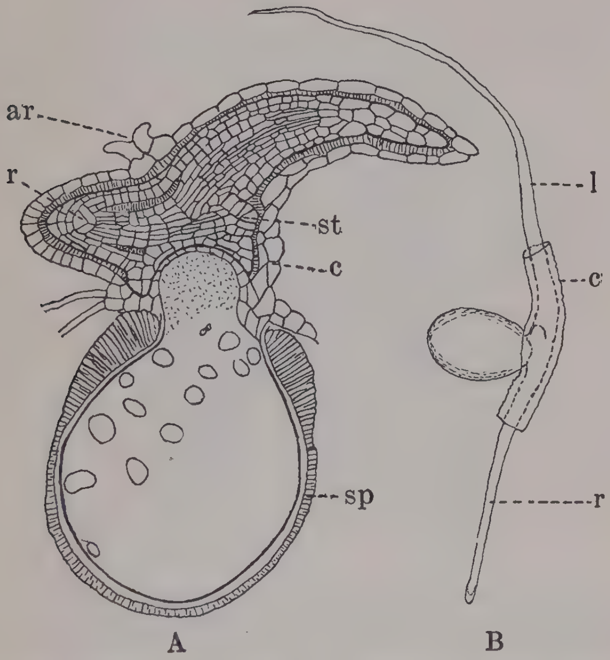

Fig. 248.—Marsilia and Pilularia. A, embryo of Pilularia still enclosed within the calyptra, *cal; ar*, neck of archegonium; *l*, leaf; *st*, stem; *r*, root; *f*, foot; *sp*, spore. B, young sporophyte of Marsilia still attached to spore and partly enclosed in the calyptra, *c*. × 12. (A, from Campbell's "Mosses and Ferns." By permission of the Macmillan Company, Publishers.)

In neither micro- nor megagametophyte do the primordia of the chloroplasts develop chlorophyll unless the life of the gametophytes is prolonged. Sometimes, however, the megagametophyte will send out rhizoids, and chlorophyll will be developed to a limited extent.

The development of the embryo is very similar to that in a polypodiaceous fern. Fig. 248, A, is a median longitudinal section of an embryo sporophyte of Pilularia still attached to the spore and enclosed within the gametophyte. In (B) is shown the young sporophyte of Marsilia, in which the first root and leaf have broken through the calyptra (*c*). The whole bears a striking resemblance to the seedling of certain seed-bearing plants.

Salviniaceae.—The two genera, Salvinia and Azolla, are small floating aquatics. Azolla occurs in the southern states, developing in large quantities on the surface of quiet stretches of water. It occurs also in California. European species of Salvinia occur also in a few places in the United States. The slender stem in Salvinia is concealed by the leaves, which are of two kinds. The larger, dorsal leaves, a centimeter or more in diameter, are arranged in four rows; the two rows of ventral leaves are finely dissected, the segments bearing rhizoid-like hairs. Roots are not developed in Salvinia, where they are represented physiologically by the

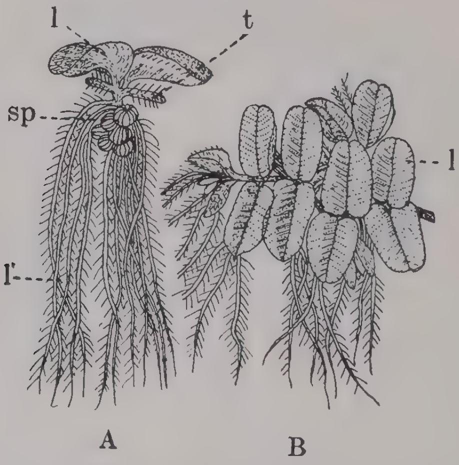

FIG. 249.—*Salvinia natans.* A, plant as seen from above. B, part of a plant bearing spores; *l*, dorsal leaves; *l'*, root-like submerged leaves; *sp*, sporocarps. (From Pringsheim.)

dissected ventral leaves (Fig. 249, B, *l'*). The leaves of Azolla are in two dorsal rows. They are very small and moss-like. Roots are present in Azolla. Rounded sporocarps are developed in both Salvinia and Azolla, those of the one differing considerably from those of the other, and from that of Marsilia. The gametophytes are greatly reduced, being similar in character to the gametophytes of Marsilia.

Class II. Equisetales

The living representatives of the second class of Pteridophytes, the Equisetales, are included in the one genus, Equisetum, of which there are about twenty-four species. Fourteen of these are said to occur in the United States.

Sporophyte.—The outstanding characteristic of the sporophyte, by which it is distinguished from the ferns, lies in the fact that the hollow shoots are jointed, and the rudimentary leaves appear as toothed sheaths at the joints (Fig. 250, A). The sporophylls are always aggregated into a cone at the apex of the shoots, and the spores are provided with hygroscopic appendages, the elaters (Fig. 251, B, C, D).

The main stem is an underground rhizome, showing the same differentiation into nodes and internodes as its aerial branches (A, B). From each node of the rhizome, which bears a sheath of leaves, arise the roots, branches, and aerial shoots. At the nodes rounded tubers are not infrequently formed, which may remain dormant or develop roots and shoots.

In some species, as in *Equisetum arvense*, two sets of aerial shoots are developed, spore-bearing and foliage shoots. The spore-bearing shoots (B), which appear in early spring, are colorless or reddish brown in color, little or no chlorophyll being developed. After the spores are shed these shoots wither and disappear. As

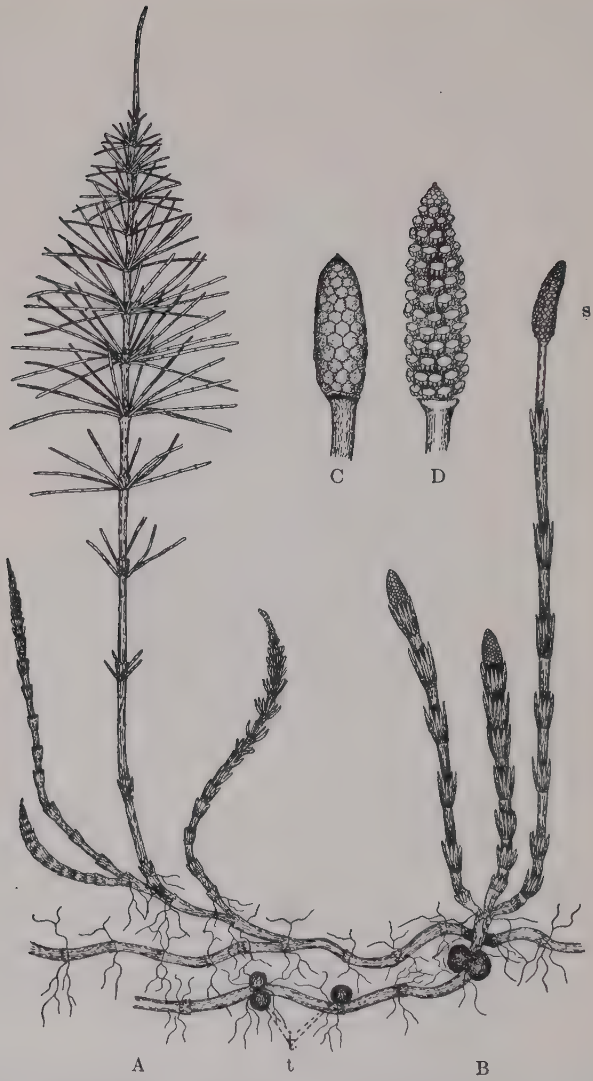

FIG. 250.—*Equisetum arvense.* A, B, vegetative and spore-bearing portions of the sporophyte; *t*, tubers on rhizome. C, spore-bearing cone almost mature. D, spore-bearing cone with axis elongated, enabling the sporangia to separate and open.

the spore-bearing shoots vanish, the foliage shoots (A) begin to appear above the ground. The latter are green and much branched. When about mature they present the appearance of a well groomed horse's tail, especially when held in an inverted position. The leaves of these shoots are reduced to small teeth forming a sheath at each joint. The photosynthetic work of the plant is performed mainly by the tissues of the stem. Such stems are termed *cladodia.*

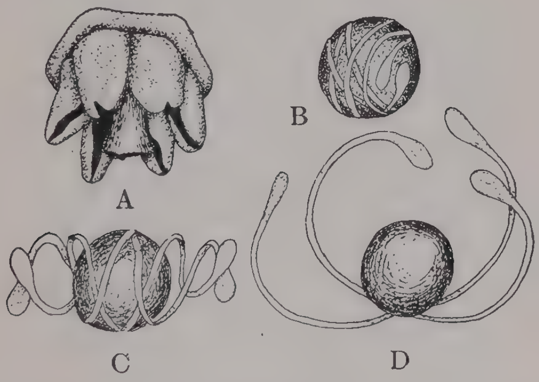

Fig. 251.—*Equisetum arvense.* A, sporophyll. B to D, spores with elaters. B, moist spore with elaters wound around it. C, elaters partly expanded. D, elaters expanded, when dry. (B, C, D, after Wassidlo.)

In other species, such as *E. hyemale* and *E. laevigatum,* only one kind of aerial stem is developed. These are reed-like and may be branched or unbranched, the spore-bearing branches ending in a cone (Fig. 252). Owing to the large quantity of silica in the cellwalls, these reed-like stems were gathered in colonial days and used in scouring metal vessels,—hence the name, *scouring rush.*

The Sporophylls.—The sporophylls are umbrella-shaped and arranged in close circles at the ends of the shoots, forming a cone. The blades of the sporophyll, because of mutual pressure, are usually hexagonal. At the edge, on the under side of the hexagonal blade, are a number of pendent, sac-like sporangia. Each sporangium opens by a longitudinal slit on the inner side (Fig. 251, A). When the spores are mature the axis of the cone elongates, thus freeing the sporophylls and permitting the spores to fall out (Fig. 250, D).

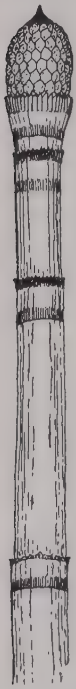

FIG. 252.—*Equisetum hiemale.* Distal end of aerial branch ending in a cone.

The outer coat of the spore is split into four strips, which, when moist, are coiled around the cell (Fig. 251, B). When dry they straighten out somewhat and appear as four strips attached to the spore (C, D). The adaptive function of these so-called *elaters* seems to be to insure the dispersal of the spores in groups. When the sporangium opens the elaters tend to become entangled with the result that the spores fall out in clusters, and, in that form, may be blown about by the wind. The result is that several spores may be deposited close to one another, and, since the gametophytes are usually dioecious, the probability of fecundation being accomplished is greater than were the male and female prothallia removed from one another by considerable distances.

Structure of the Stem.—The shoots of Equisetum are very porous in structure, the vascular system being scantily developed. Running lengthwise in the internodes are a large central cavity in the pith, a circle of similar cavities in the cortex, and one in each vascular bundle. These cavities are formed by the disorganization of the tissues. The vascular bundle is reduced to a few protoxylem elements and a few sieve elements. A diagram of a cross section of the spore-bearing shoot of *Equisetum* *arvense* is shown in Fig. 253. Fig. 254 is a cross section of a vascular bundle with its large water passage (*car*).

The Gametophyte.—The gametophyte of Equisetum is a somewhat flattened, irregularly branched or lobed, green structure resembling, in general, certain fern prothallia or the gametophytes of certain liverworts (Fig. 255). The gametophyte is generally dioecious. The male plants are often smaller and the antheridia develop earlier than the archegonia. The antheridia and archegonia bear a close resemblance to those organs in the eusporangiate ferns.

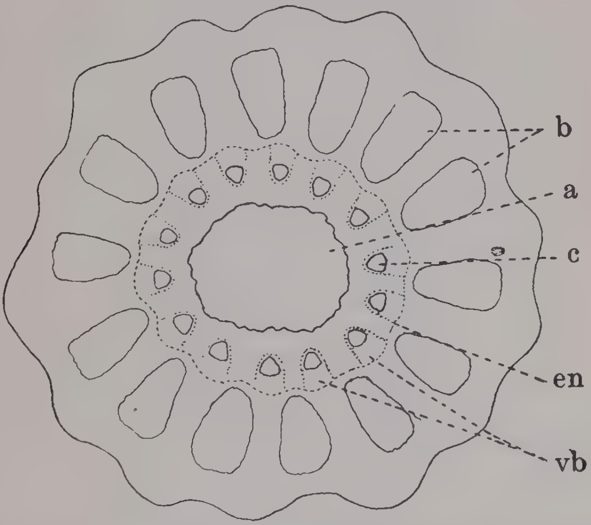

Fig. 253.—*Equisetum arvense.* Diagram of a cross section of an internode of a spore-bearing shoot; *a*, large central cavity of the pith; *b*, similar cavities (vallecular canals) in the cortex; *c*, cavities, water passages (carinal canals) in the vascular bundles; *en*, endodermis; *vb*, vascular bundle.

Class III. Lycopodiales. Club Mosses

The typical Club Mosses are readily distinguished from the other Pteridophyta, especially the ferns, by the moss-like appearance of the sporophytes, which

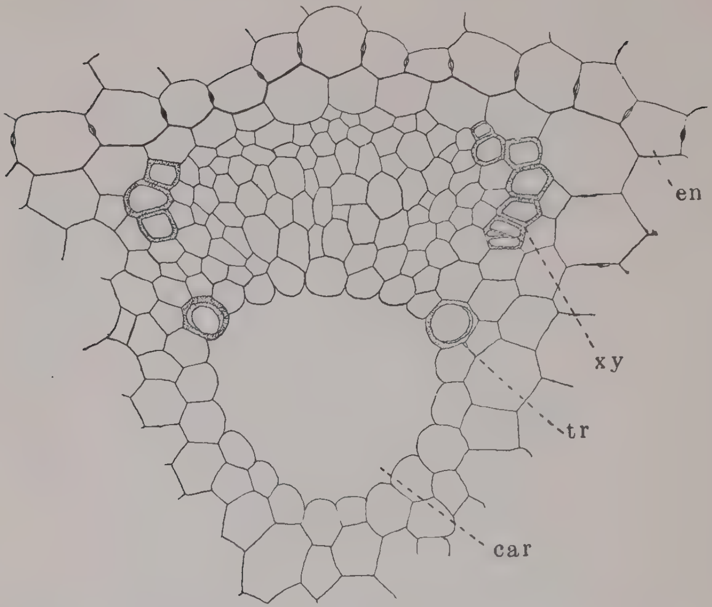

FIG. 254.—*Equisetum arvense.* Cross section of vascular bundle of spore-bearing shoot; *en*, endodermis; *xy*, xylem; *tr*, remaining primary tracheids of the xylem; *car*, carinal canal, water passage.

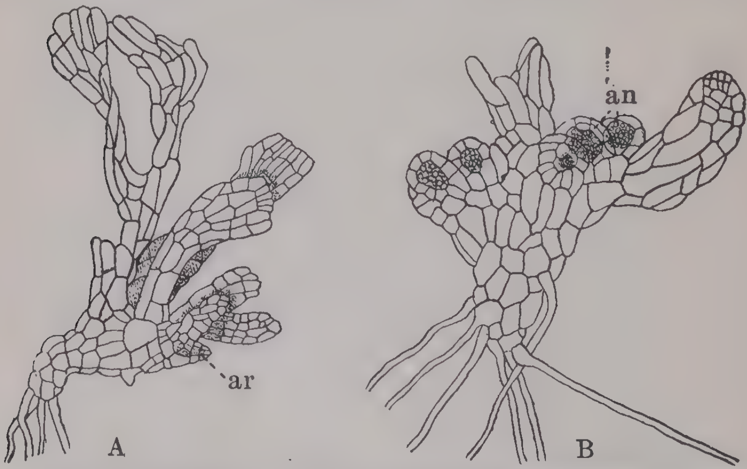

FIG. 255.—Equisetum. A, male, and B, female, gametophytes; *ar*, archegonium; *an*, antheridia. (From Campbell's "Mosses and Ferns." By permission of the Macmillan Company, Publishers.)

possess small, moss-like leaves that thickly clothe the stem of the younger parts.

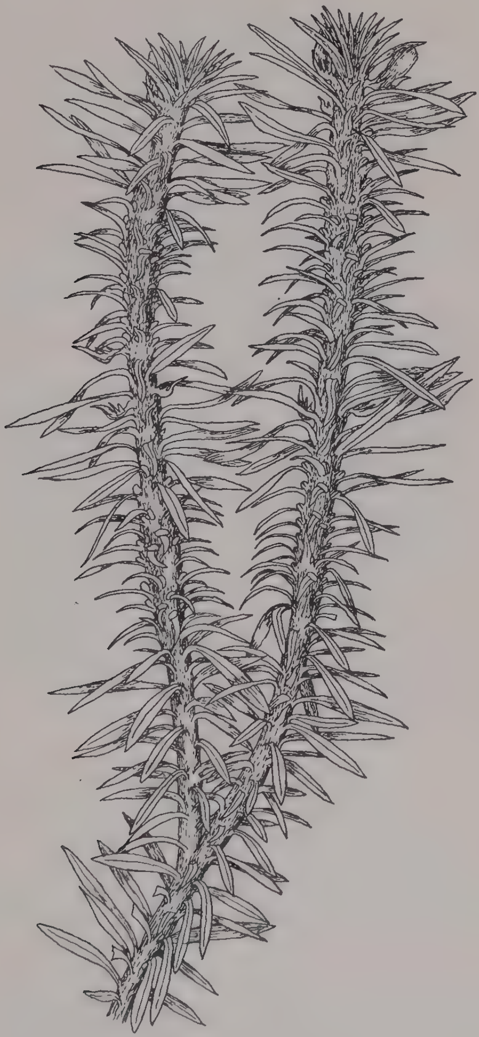

FIG. 256.—*Lycopodium lucidulum* Michx.

The living representatives comprise four families: Lycopodiaceae, Psilotaceae, Selaginellaceae, and Isoetaceae, although there are valid reasons for placing the last named family in a class by itself.

Lycopodiaceae.—The sporophyte of Lycopodium consists of an upright stem, as in *L. lucidulum* (Fig. 256), or a slender, creeping rhizome, from which spring upright branches, as in *L. clavatum* or *L. complanatum* (Fig. 259). Branching is either monopodial or dichotomous. The leaves are very simple in structure, and are traversed by a single median vascular bundle. The roots may branch dichotomously. In some species the sporophyte is propagated vegetatively by small leafy buds (gemmae), which fall off and grow into separate plants (Fig. 258, A, B).

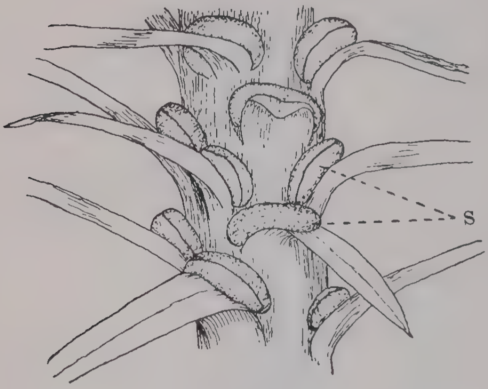

FIG. 257.

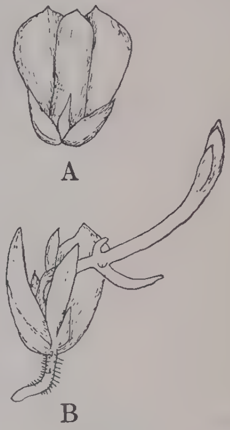

FIG. 258.

FIG. 257.—*Lycopodium lucidulum* Michx. Portion of stem enlarged, showing position of sporangia, *s*.

FIG. 258.—Lycopodium. A, gemma of *L. lucidulum*. × 4. B, young plant of *L. selago* arising from germinating bud. × 4. (A, from Campbell's "Mosses and Ferns." By permission of the Macmillan Company Publishers. B, from Cramer.)

Sporangia.—The sporangia are somewhat kidney-shaped, and borne singly on the adaxial side of the sporophylls, which may differ very little from the regular foliage leaves, as in *L. lucidulum* (Fig. 257, *s*). In certain species the sporophylls are closely aggregated

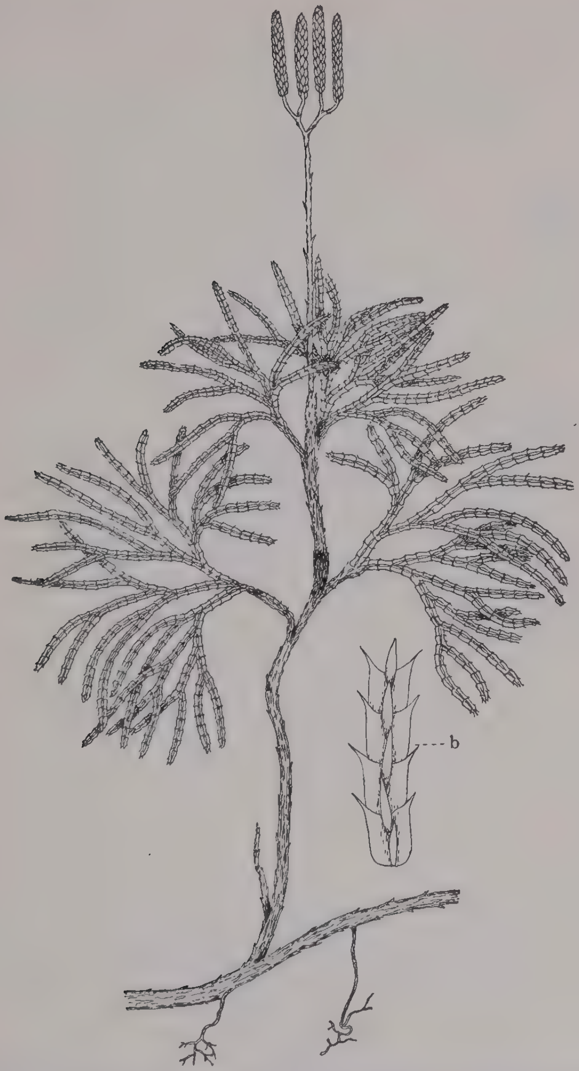

FIG. 259.—Portion of the sporophyte of *Lycopodium complanatum flabelliforme* Fernald; *b*, portion of branch, enlarged to show arrangement of leaves.

into cones (strobili) borne at the ends of upright shoots (Fig. 259). The spores are of one kind.

The Gametophyte.—In certain species the gametophyte is a small, flattened, tuber-like structure similar to that of Botrychium, growing saprophytically beneath the surface of the ground, as in *L. annotinum* (Fig. 260, *g*). In other species, as in *L. complanatum*, the gametophyte is an upright, somewhat cylindrical body terminating in a crown of leaf-like lobes containing chlorophyll, in which the sex organs are located (Fig. 261, A, B). Chlorophyll is not developed in the underground portion. In cells of a definite region an endophytic fungus occurs, which assists the gametophyte in securing nourishment from the soil.

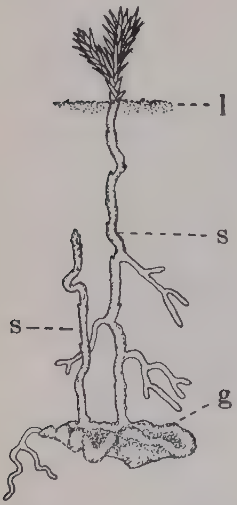

Fig. 260.—*Lycopodium annotinum.* The flattened gametophyte, *g*, bearing two sporophytes, *s*; *l*, level of the soil. (From Bruchmann.)

As stated, the sex organs are borne on the crown or on the upper side. The antheridium is more massive than in the ferns, resembling those of Equisetum or of the Ophioglossaceae. The archegonia are also larger than those of the fern, bearing a strong resemblance to those of the liverworts.

In the development of the young sporophyte in a certain species, a small, tuber-like stem, called a *protocorm,* is first formed. From it the roots and stem later develop. Several sporophytes may be formed on one gametophyte. The gametophyte shown in Fig. 260 bears two visible sporophytes, one larger than the other. The development of the young sporophyte is slow, being dependent upon the gametophyte for a long time.

Phylloglossum.—The one species, *Phylloglossum Drummondii*, native to Australia, is a small plant resembling a young sporophyte of Lycopodium (Fig. 262). The spores are borne in a small strobilus at the end of a short, naked stalk.

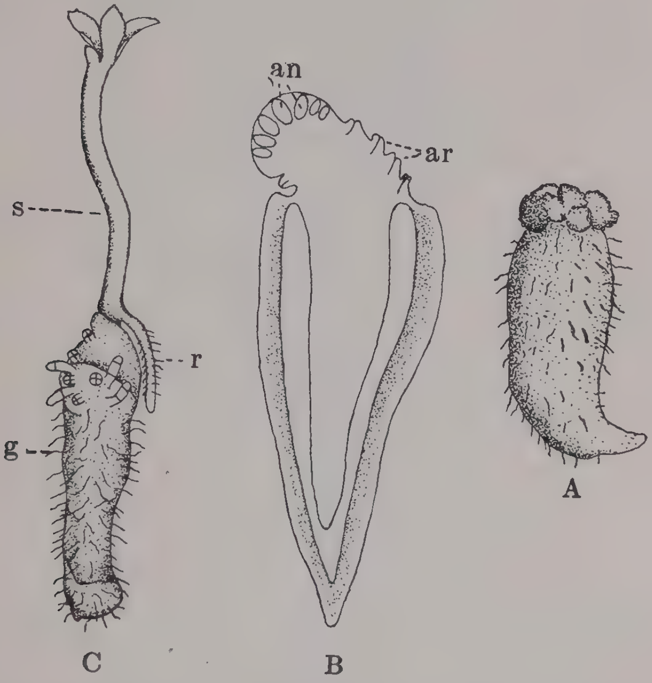

Fig. 261.—Gametophytes and young sporophyte of Lycopodium. A, B, tuberous gametophyte of *L. complanatum;* B, in longitudinal section; *an*, antheridia; *ar*, archegonia; the shaded region indicates the location of the endophytic fungus. C, *L. lucidulum; g*, gametophyte; *s*, young sporophyte; *r*, root. (A, from Bruchmann; B, C, from Spessard.)

Psilotaceae.—This is a small family of plants, mostly tropical. One species (*Psilotum triquetrium*) is found in Florida. The sporophyte is usually epiphytic. It is a slender, creeping, leafless stem. The roots, which develop from rhizome-like shoots, branch dichotomously.

Specimens are sometimes cultivated in large conservatories along with other exotic plants.

Selaginellaceae.—The sporophyte of Selaginella bears a close resemblance to that of certain species of Lycopodium. In some species the leaves are all alike (as in *S. arenicola* Underw.), and arranged spirally on the stem; while in others they are arranged in four rows, two rows of large leaves and two of small ones, as in *S. krausiana* (Fig. 264). A characteristic of Selaginella is the development of a small outgrowth at the base of the leaf on the adaxial side, known as a ligule.

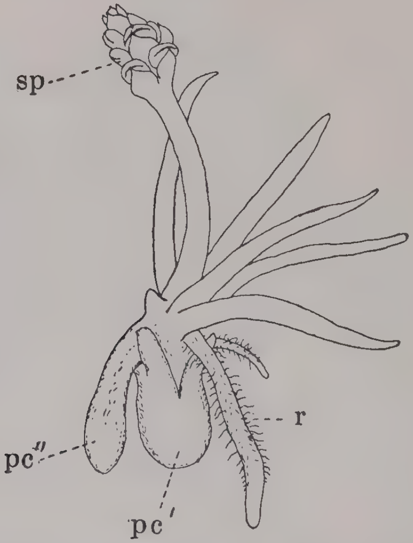

Fig. 262.—A plant of *Phylloglossum Drummondii*, x about 3; *sp*, sporangia; *r*, roots; *pc'*, protocorm; *pc''*, secondary protocorm. (From Bertrand.)

Selaginella differs markedly from Lycopodium, however, in that it is heterosporous. The sporophylls are usually aggregated into cones borne at the ends of the branches (Fig. 265, A). Both microsporangia and megasporangia are borne in the same cone. Sporangia are borne singly on the stem just above the leaf axils.

Each sporophyll subtends, therefore, but one sporangium. In most species the lower sporangia bear the megaspores, four to a sporangium, while those higher in the strobilus bear very many microspores (Fig. 265,

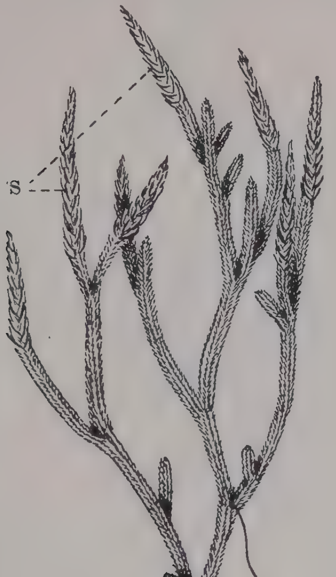

Fig. 263.—*Selaginella arenicola* Underw. Habit of sporophyte; *s*, spore-bearing cones.

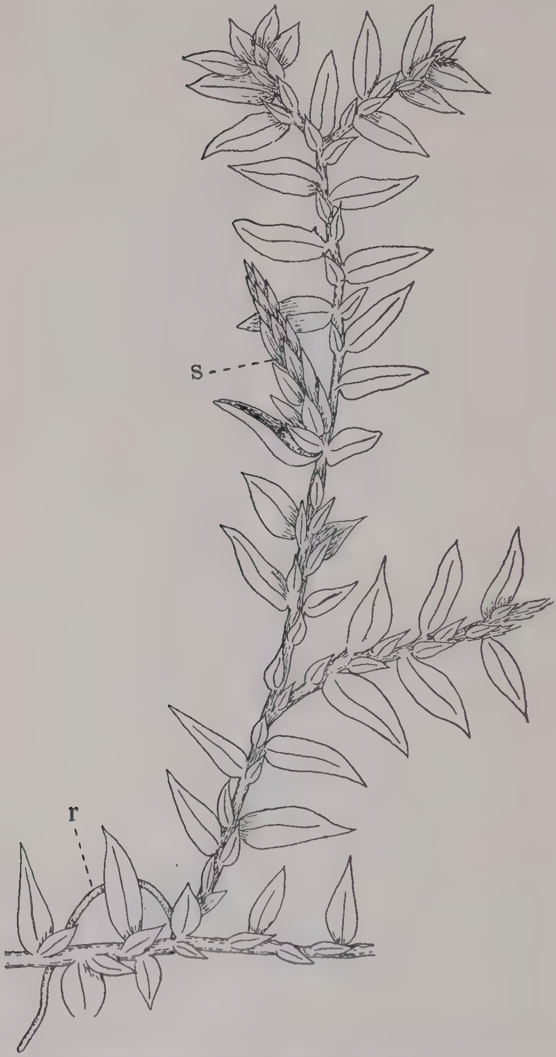

FIG. 264.—*Selaginella krausiana.* Branch of sporophyte with spore-bearing cone, *s*; *r*, root. (From Campbell's "Mosses and Ferns." By permission of the Macmillan Company, Publishers.)

B). The vast majority of species are tropical, but a few occur in temperate regions. *Selaginella apus* occurs

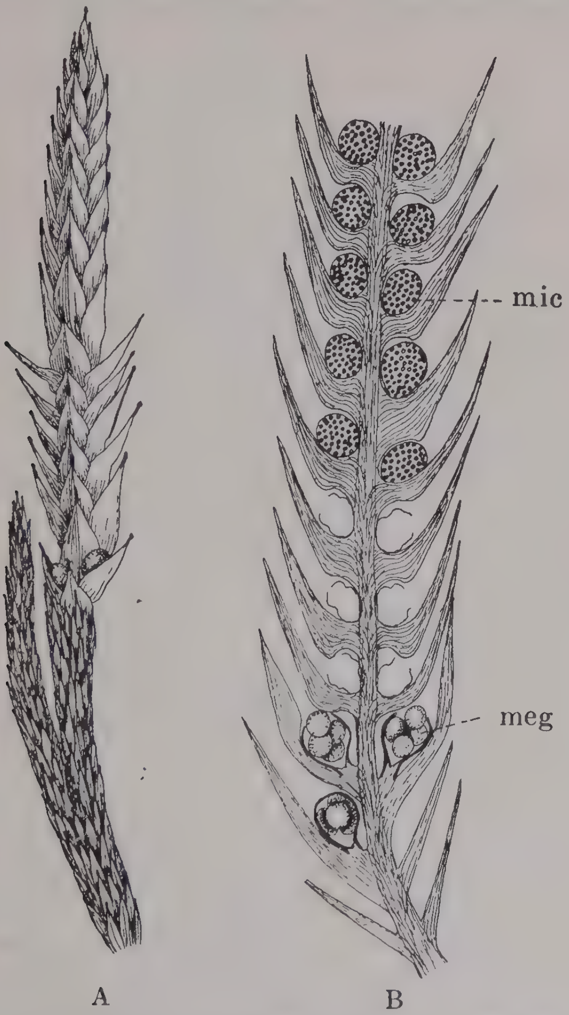

FIG. 265.—*Selaginella arenicola* Underw. A, end of a branch with a spore-bearing cone, much enlarged. B, longitudinal section of cone; *meg*, megasporangium; *mic*, microsporangium.

in Indiana, growing on moist earth along the shores of lakes. As a rule they have a profusely branched, creeping stem, forming moss-like mats; some, however, climb on adjacent plants and develop stems several meters in length. Some species grow erect. Those like *S. lepidophylla* and *S. rupestris*, growing in dry situations, are capable of resisting drought for many months. These are among the specimens known as "resurrection plants" sold in certain curiosity shops.

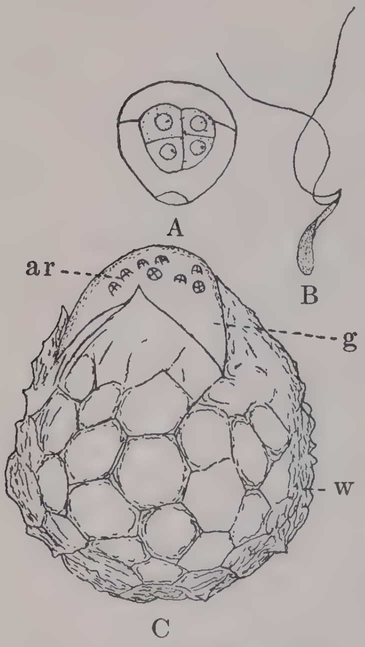

FIG. 266.—*Selaginella krausiana.* A, microgametophyte not quite mature; B, sperm. C, megagametophyte, *g*, within the old spore wall, *w*, the protruding part bearing the archegonia, *ar*. (A, B, from Belajeff; C, from Campbell's "Mosses and Ferns." By permission of the Macmillan Company, Publishers.)

The Gametophyte.—The plants being heterosporous, there are naturally two kinds of gametophytes, the male, microgametophyte, developing from the microspore, and the female, megagametophyte, produced by the megaspore.

The microgametophyte is very small, merely filling the cavity of the spore, and resembling that of Marsilia (Fig. 266, A). It consists of a central mass of sperm-bearing cells surrounded by a single layer of cells which finally break down, liberating the sperms. Chlorophyll is not developed. In reality the microgametophyte seems to consist of a single antheridium and a vegetative cell, or so-called *prothallial cell*. The sperms are biciliate.

The megagametophyte is also largely confined to the megaspore, protruding only slightly when mature through an opening in the thick spore wall. Chlorophyll is not developed at all, or only to a very limited degree in that portion protruding from the spore (Fig. 266, C). In both micro- and megaspores sufficient food is stored for the complete development of the gametophytes, and, in the case of the megaspore, for the early development of the embryo sporophyte as well.

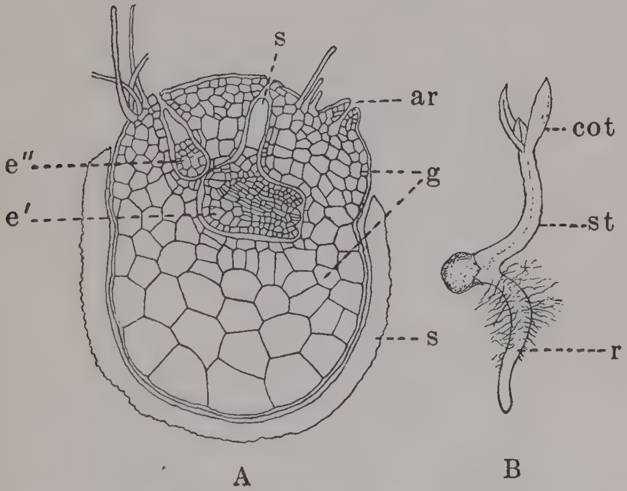

Fig. 267.—Selaginella. A, *S. Martensii*, vertical section of megagametophyte, with two embryo sporophytes, *e′* and *e″*, partly enclosed by the wall of the megaspore, *s*; *g*, gametophyte; *sus*, suspensor; *ar*, archegonium. B, *S. krausiana*, young sporophyte still attached to the spore; *cot*, cotyledons; *st*, stem; *r*, root. (A, adapted from Strasburger, after Pfeffer. B, From Campbell's "Mosses and Ferns." By permission of the Macmillan Company, Publishers.)

Fig. 267 represents a section through a megagametophyte enclosing two embryo sporophytes. As in the case of the fern, the embryo, while enclosed in the gametophyte, shows the three distinct regions, foot, root, and stem. The stem at the stage in question shows the beginning of two young leaves; each will bear a ligule at its base. There is an additional organ not present in the embryo of the ordinary ferns, but present in some of the Ophioglossaceae, namely, the "suspensor" (Fig. 267), or in reality, the *pusher*. As in Lycopodium, the suspensor is the first part of the embryo to be differentiated, and it seems to push that part from which foot, stem and root develop, down into the tissue of the gametophyte. We have here, therefore, a tolerably well differentiated embryo sporophyte completely surrounded by the tissues of the gametophyte. More than one sporophyte may be developed on a gametophyte. The structure bears a striking resemblance to a seed of certain seed-bearing plants, and, for that reason, Selaginella has become a fruitful field for speculation with reference to the origin of the seed habit. We are content here to call attention to certain points of resemblance between the condition shown in Fig. 267, A and a seed, and at the same time to indicate what Selaginella lacks in producing a real seed as found in the Spermatophyta.

Since the tissue of the megagametophyte is homologous with the endosperm in certain seeds, as in Gymnosperms, the embryo sporophyte of Selaginella, with its surrounding gametophyte tissue, is comparable to the embryo and surrounding endosperm of a seed. However, Selaginella falls short of developing a seed in the following respects: There is nothing homologous with a definite seed coat, and the embryo does not pass into a dormant state as in the seed of seed plants. In all Pteridophytes the development of the embryo from the zygote is a continuous and uninterrupted process until the embryo has established itself in the soil.

The foregoing statements are not intended to convey the idea that Selaginella represents the ancestral condition of the seed plants. Their purpose is merely to show what progress Selaginella has made toward the seed habit. There are reasons to believe that seed plants took their origin among certain heterosporous Pteridophyta. Heterospory is a condition found in all seed plants, and their ancestors were undoubtedly heterosporous. With reference to the embryo and its

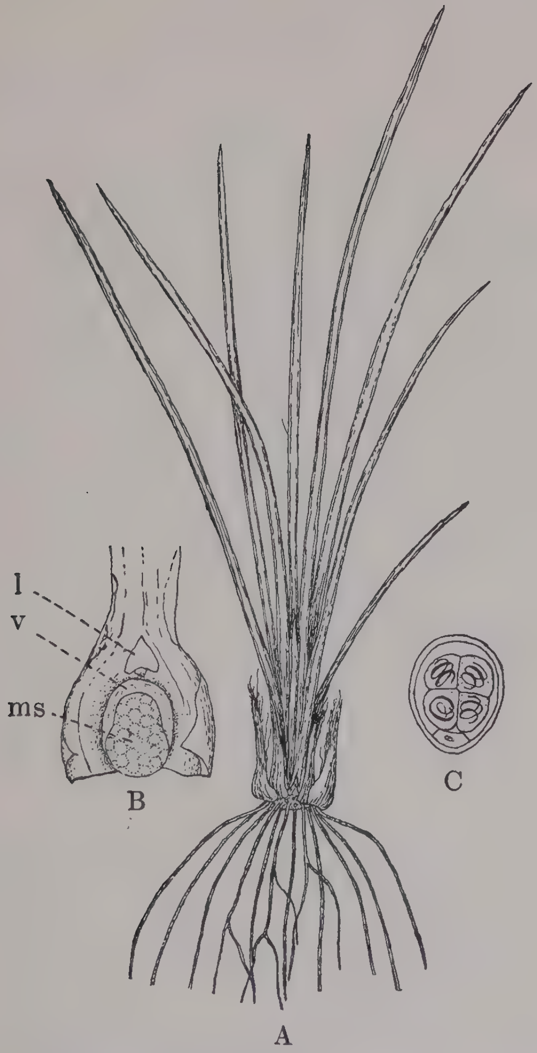

FIG. 268.—Isoetes. A, habit of sporophyte. B, base of leaf with megasporangium, *ms*; *l*, ligule; *v*, velum. C, microgametophyte, consisting of one vegetative cell, and one antheridium with four sperms. (C, from Campbell's "Mosses and Ferns." By permission of the Macmillan Company, Publishers.)

surrounding gametophyte, certain seed characters may be recognized in the Ophioglossaceae.

Isoetaceae.—This family is represented by the genus Isoetes, species of which occur in our flora. The plants are commonly known as Quillworts. They bear no external resemblance to other Pteridophyta. The sporophyte resembles a tuft of grass or small rushes (Fig. 268, A). It consists of a very short, flattened stem bearing numerous roots and onion-like leaves. Each leaf has a broad base, just above which is the ligule (Fig. 268, B, 1). The leaf bases overlap and conceal the stem. Isoetes is heterosporous. The sporangia are borne at the base of the leaves on the adaxial side. The outer leaves of each cycle bear microspores, and the inner, megaspores. The innermost leaves, which are sterile and not fully developed, separate one year's growth from the next. The oval sporangium is sunk in a depression whose margin (*v*) may almost completely cover the sporangium (*ms*). The gametophytes are similar in character to those of Selaginella. The structure and development of the whole plant suggests in many ways a monocotyledonous seed plant. The microgametophyte is reduced to a single prothallial cell and an antheridium bearing four biciliate sperms (Fig. 268, C).

Fossil Pteridophyta.—In the period of geologic time known as the Paleozoic age, the majority of Ferns, as revealed by known fossils, were plants resembling the living Marattiaceae. Many of the Horse Tails and Club Mosses attained the size of lofty trees, constituting the forests of the humid regions of the earth. Those that exist today may be looked upon as the degenerate remnants of the gigantic forms once prevailing in great numbers,—the mere ruins of a magnificient flora. The Pteridophyta of that time contributed largely to the formation of the coal deposits of the earth.

CHAPTER XVII

SPERMATOPHYTA

The Spermatophyta include all those plants that bear seeds as well as microspores and megaspores. There are two great groups, Gymnosperms and Angiosperms. In the Gymnosperms the seeds are borne on open megasporophylls (Carpels), as in the pine cone, etc., while Angiosperms produce seeds on megasporophylls that form closed cavities. In the common pea, for example, the pod represents the megasporophyll that completely encloses the seeds.

GYMNOSPERMS

As a representative of the gymnosperms we may select for study some pine, such as the Austrian or black pine (*Pinus nigra* Arnold), the Scotch pine (*P. sylvestris* L.), or the white pine (*P. strobus* L.).

The Pine Tree, the Sporophyte.—A typical pine tree, such as the white pine (Fig. 269) has a main stem, or trunk, extending from the ground straight up to the tip of the tree, and ending in a terminal bud. The terminal bud dominates all the other buds, and from near its base arise a circle of lateral buds. The trunk is continued straight downwards into the earth as a tap root, from which spring numerous branching secondary roots.

From the trunk grow out at regular intervals more or less horizontally, long branches that tend to be arranged in circles. They do not form perfect circles, or whorls, because they may arise at slightly different levels. The branches springing directly from the main trunk develop other branches varying in length, which tend to spread out in the intervening spaces. All of these long branches are of unlimited growth and end in a terminal bud. One or more lateral buds may also be present near the base of the terminal bud.

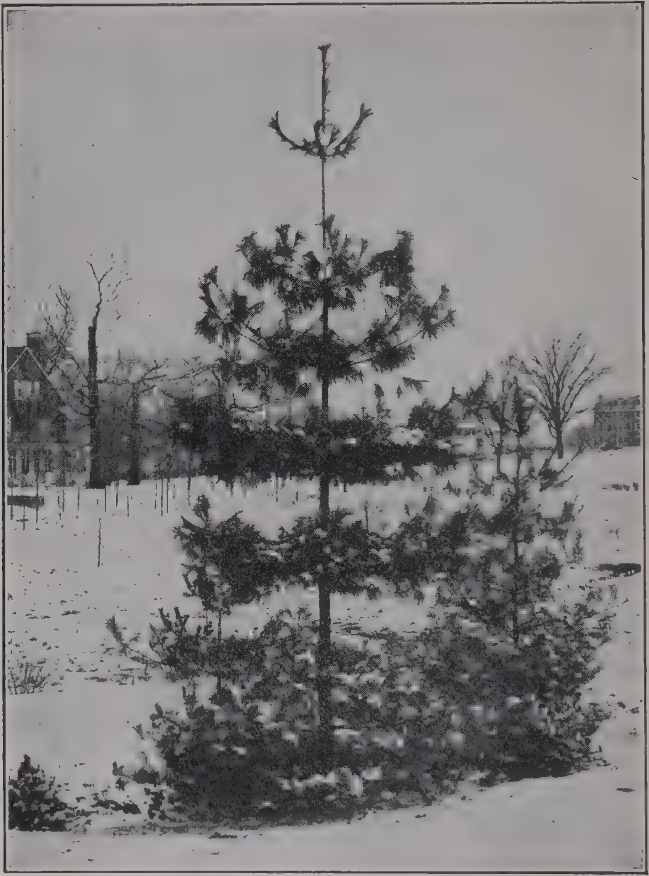

Fig. 269.—*Pinus strobus.* Young tree of the white pine. Note the tendency of the branches to arise in whorls on the main stem.

All of the long branches bear numerous very short dwarf shoots of limited growth, each of which, in the Scotch and Austrian pine, ends in two needle-shaped foliage leaves. The dwarf shoots of the white pine each bear five needle-shaped foliage leaves. The dwarf shoots bear also a number of small scales, forming a sheath at the base of the leaves (Fig. 287). In the young tree foliage leaves arise also from the main trunk and from the long branches.

The older and lower branches of the pine tree are longer. Higher up the branches are successively shorter, so that the result is the handsome, conical, or pyramidal shape of large trees. With age many pine trees form a flat, spreading top, especially if grown in the open.

The terminal bud of the main axis contains the growing end of the stem which persists throughout the life of the tree unless the bud be removed or injured. If the end of the main axis be injured or destroyed, one of the long branches of the next circle below will assume an upright position and continue growth straight upwards as the main stem.

Each bud on the long branches is provided externally with scale-like leaves, bud scales. The bud scales enclose whatever young parts are developing from the growing point of the stem. The pine produces in all, three kinds of leaves, scale, foliage, and spore-bearing leaves, or sporophylls.

The foliage leaves of the Austrian pine live three or four years. Consequently, after the tree is four years old, leaves are shed annually. As in the case of deciduous trees, a new crop of leaves is produced annually.

The Pine Cone.—The fruit of the pine tree is the seed-bearing strobilus (Fig. 270, A). This strobilus consists of an axis, on which are laterally borne and closely aggregated, hard, horny scales, the carpels (Megasporophylls), which are brown in color when mature. About half of the carpels of the cone,—those at the basal end,—are aborted and bear no seeds. On each carpel of the upper portion of the cone one or two seeds are developed at its base on the adaxial side (Fig. 270, B). After the cone is mature the carpels spring apart liberating the seeds. In our climate this takes place, as a rule, in the Austrian pine, in January or February.

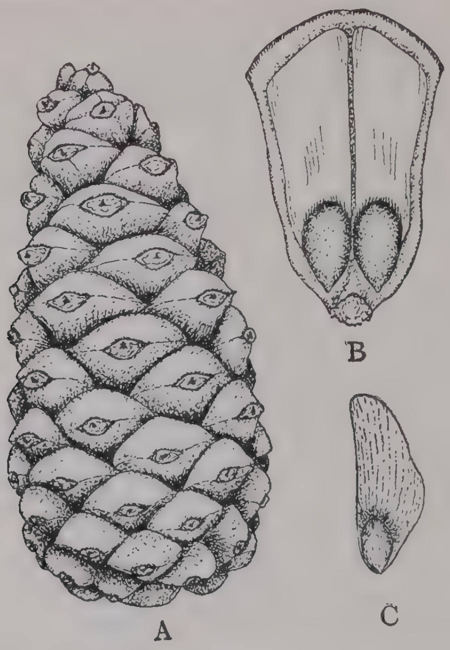

Fig. 270.—*Pinus nigra*. A, full grown carpellate cone, about June 1, of the second year. B, adaxial view of one carpel with the two winged seeds in position. C, a mature seed.

The Seed.—The seed of the pine in question is a somewhat flattened, oval structure, provided with a thin, brown, membranous wing (Fig. 270, C). The wing is derived from the adaxial surface of the carpel. The seed consists of a centrally placed embryo sporophyte, surrounded by the megagametophyte, called the endosperm, and the shell-like cover, the seed coat (Fig. 271, A). The seed coat is separable into two visible layers, the outer, thick, hard part, and a thin, brown, papery membrane. At the lower end of the seed is a small opening in the seed coat, the micropyle (Fig. 271, A, *m*.)

The cylindrical embryo bears at its upper end a number of leaves, the cotyledons (Fig. 271, B, *c*). The larger part of the axis below the cotyledons is the stem, or hypocotyl, and from the lower end next to the micropyle the root will develop. At this end of the embryo may sometimes be seen a fine, whitish, coiled thread, the suspensor (Fig. 271, B, *s*). The growing point of the stem is surrounded by the bases of the cotyledons.

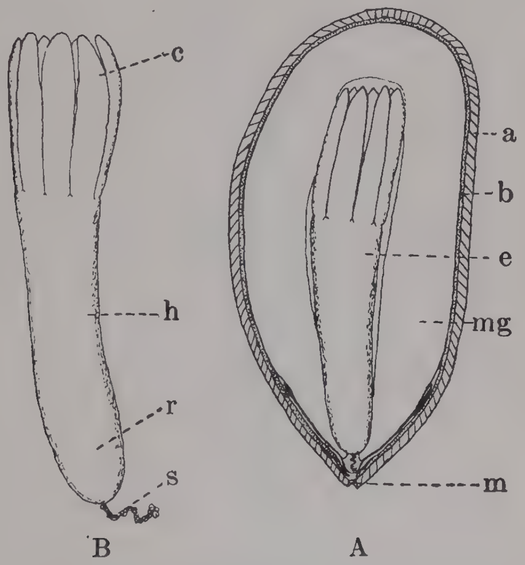

FIG. 271.—*Pinus edulis.* A, longitudinal section of a seed with the whole embryo in position; *a*, stony layer of seed coat; *b*, brown, membranous layer of seed coat; *mg*, megagametophyte, or endosperm; *e*, embryo; *m*, micropyle. B, embryo removed from endosperm and more enlarged; *c*, cotyledons; *h*, hypocotyl; *s*, suspensor; *r*, primary root.

Development of the Seed.—As stated in a preceding paragraph, seed-bearing plants produce both spores and seeds. Before seeds may be produced, flowers must be developed, for gymnosperms possess flowers as well as do angiosperms, although the latter are usually referred to as the flowering plants.

In the pine there are two kinds of flowers, which bear the two kinds of spores. These are in the form of cones, or *strobili*. The flowers that produce the microspores are composed of microsporophylls; they are called "male" flowers, or staminate flowers. Those that produce megaspores are composed of megasporophylls, and are

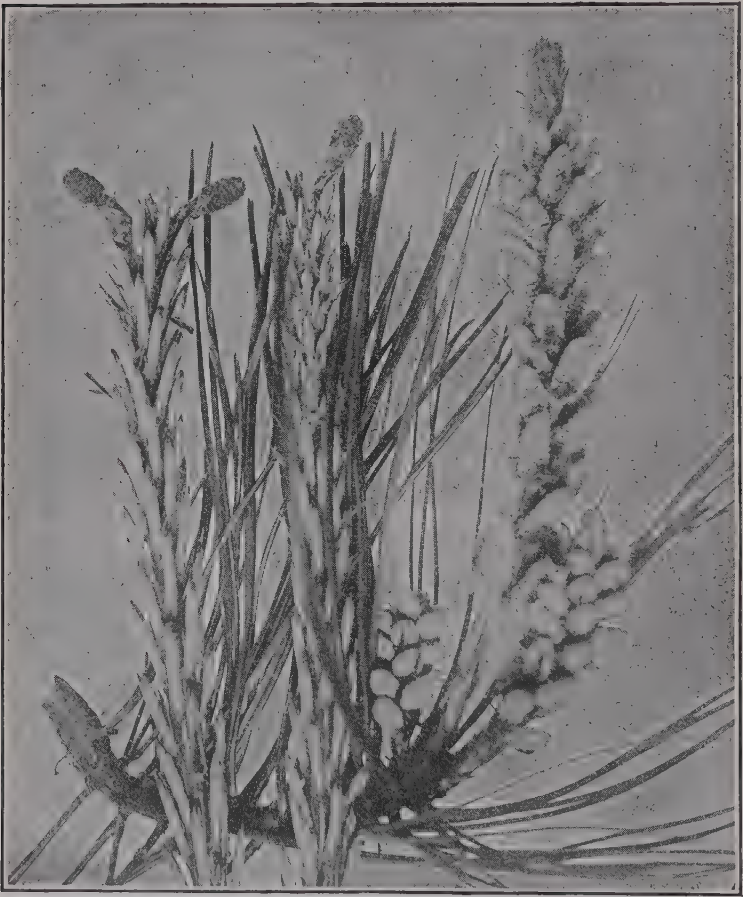

Fig. 272.—Young shoots of *Pinus sylvestris* bearing flowers; staminate strobili at the right, ovulate at the left.

commonly referred to as the "female" flowers, or ovulate flowers.

The Staminate Cone of Pinus.—In the staminate strobilus the microsporophylls are closely crowded and spirally arranged on the axis. These strobili are borne in clusters at the base of the shoot of the season's growth (Fig. 272 at the right). Each microsporophyll is somewhat triangular in shaped and bears two microsporangia (pollen sacs) on the abaxial side (Fig. 273, A). Each microsporangium, when mature, opens by means of a longitudinal slit and liberates the microspores, which

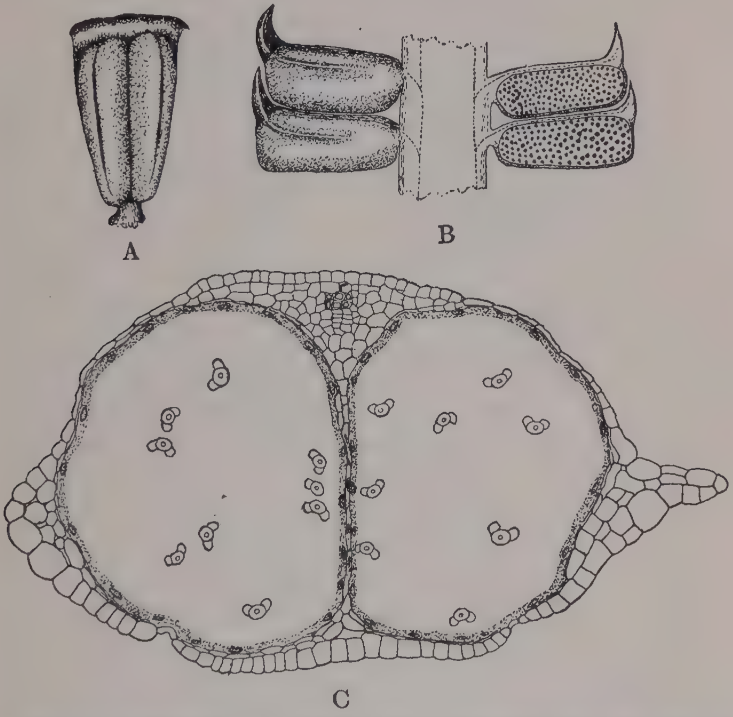

Fig. 273.—*Pinus nigra.* A, abaxial view of a microsporophyll, showing the two microsporangia, each opening by a longitudinal dehiscence. B, portion of axis of strobilus, with two sporophylls at the left in surface view, and two at the right in longitudinal section. C, cross section of sporophyll.

are more commonly known as pollen spores, or pollen grains. A cross section of a microsporophyll is shown in Fig. 273, C. From this is seen the relation of the two sporangia to the blade of the sporophyll.

The Microspore.—In the developing microsporangium the pollen spores are formed from a mass of large cells termed microspore mother-cells. Each mother-cell gives rise to four spores. As in the Pteridophyta and Bryophyta, the four spores derived from a spore mother-cell constitute a spore tetrad. The first nuclear division in the spore mother-cell is a reducing division, consequently, each microspore possesses the single number of chromosomes. Immediately following the tetrad divisions, each spore develops a firm cell wall of two layers, the outer layer being the exine, and the inner the intine. At two places on opposite sides of the spore, the exine separates from the intine, and air enters the opening. There are thus formed two inflated appendages, the "wings" of the spore (Fig. 274). Before the sporangia are mature each spore produces, by three successive divisions, a series of three small cells within, called prothallial cells. Two of these cells disorganize soon after they are formed, leaving the third, which will be known as the antheridial cell. The pollen spore at the time of the opening of the sporangium consists, therefore, of the large tube cell, and, within, at the dorsal side of the spore, the antheridial cell and the remains of two disorganized prothallial cells (Fig. 274).

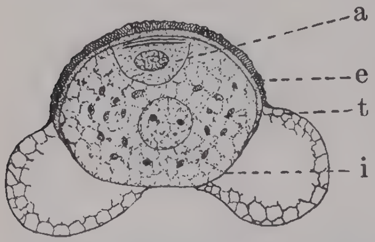

Fig. 274.—Microspore of *Pinus nigra*. *e*, exine; *i*, intine; *t*, tube cell; *a*, antheridial cell.

The Ovulate Strobilus.—The ovulate flower is a strobilus in which the megasporophylls (carpels) are also closely and spirally arranged on the axis. Each megasporophyll is also somewhat triangular in outline (Fig. 275). It consists of a small bract, from whose adaxial side, near the base, is developed the large ovuliferous scale, which later becomes the bony carpel. By the time the flower is in bloom the ovuliferous scale is larger than the bract, which is seen in the abaxial view (Fig. 275, B, *b*). The ovuliferous scale bears two megasporangia, ovules, near its base on the upper,

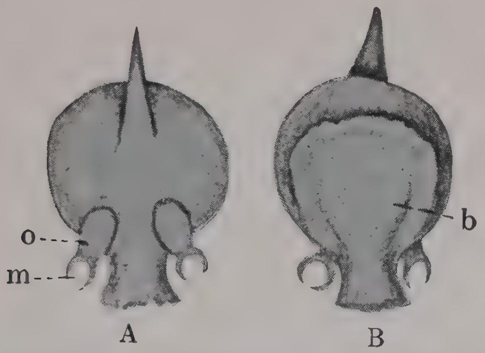

Fig. 275.—*Pinus nigra*. A, adaxial (upper) view of megasporophyll, showing the two megasporangia (ovules). B, abaxial view, showing the bract, *b*.

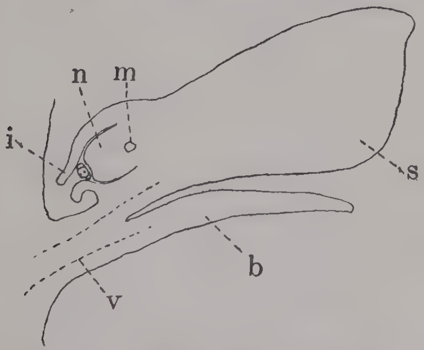

Fig. 276.—*Pinus nigra*. Outline of longitudinal section of a megasporophyll, showing attachment to axis of cone, at the time of pollination. *b*, bract; *s*, ovuliferous scale; *n*, nucellus; *m*, megaspore mother cell; *p*, pollen spore; *i*, integument; *v*, vascular bundles.

adaxial, side (Fig. 275, A, *o*). At the lower end of each ovule is a small cleft, the micropyle. The relation of bract, ovuliferous scale, and ovule is readily seen in a longitudinal section, as shown in Fig. 276. In the Austrian pine both staminate and carpellate flowers are borne on the same tree. When this is true the tree (sporophyte) is monoecious. If, as in some gymnosperms, the red cedar, for example, the staminate flowers are borne on one tree and the ovulate flowers on another, the sporophyte is dioecious.

Pollination.—When the microsporangia open the pollen is carried by the wind and gravity to the ovulate cone, and some of the spores may fall or roll down into the micropyle, where they are soon to germinate. The staminate cones now shrivel up and fall from the tree. The staminate flowers contribute only the pollen spores to the process of seed development. The ovulate cone contributes all the rest.

The Ovule, Megasporangium, at the Time of Pollination.—A median longitudinal section of the ovule at this stage will reveal the structures present. In Fig. 277, it will be seen that the ovule consists of a central mass of cells, the nucellus (*n*), surrounded by a layer of tissue four or more cells thick, the integument (*i*). The integument grows up beyond the free end of the nucellus, but does not close completely. The small opening (*m*) remaining is the micropyle, in which one or more pollen spores (*p*) may be found. Deeply situated in the nucellus is the well defined megaspore mother-cell (*mc*). From this cell a tetrad of four, potential megaspores is formed, but only one, as a rule, is functional, the other three being consumed as food by the functional megaspore, which gives rise to the megagametophyte, endosperm.

The first nuclear division in the megaspore mother-cell is a reducing division, hence the nucleus of the megaspore contains the single number of chromosomes. The nuclei of the megagametophyte contain, therefore, the single number of chromosomes.

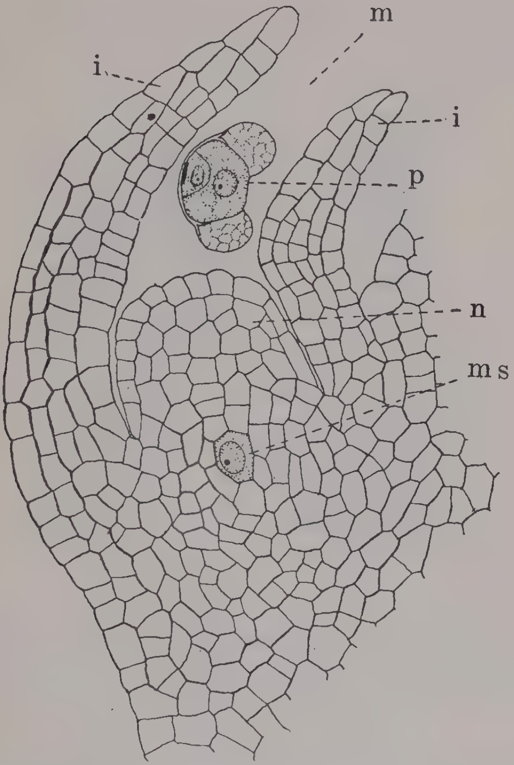

Fig. 277.—Pinus. Longitudinal section of an ovule at right angles to the flat surface. *n*, nucellus, or megasporangium proper; *ii*, integument; *m*, micropyle; *p*, pollen spore; *ms*, megaspore mother cell.

The Ovule at the End of the First Season's Growth.—Two years are necessary for the complete development of the pine seed. During the first summer following pollination the ovulate cone increases in size from that of Fig. 272, left, to that of Fig. 278, A. It is evident that little growth occurs during the first summer.

During the first season the microspores and megaspores begin their development into gametophytes. A median longitudinal section of an ovule at or near the close of the first year's growth is shown in Fig. 279. The micropyle is now closed. The tube cell of the germinating pollen spore has formed a short tube (*pt*), which takes a downward* course in the nucellus. The antheridial cell is unchanged. The megaspore (*ms*) has greatly enlarged at the expense of the nutritive tissue immediately surrounding it, the *spongy tissue*, which is specially developed from the nucellus. In the megaspore a number of nuclei may be present. The pollen spore and its developing tube is the *microgametophyte*, and all

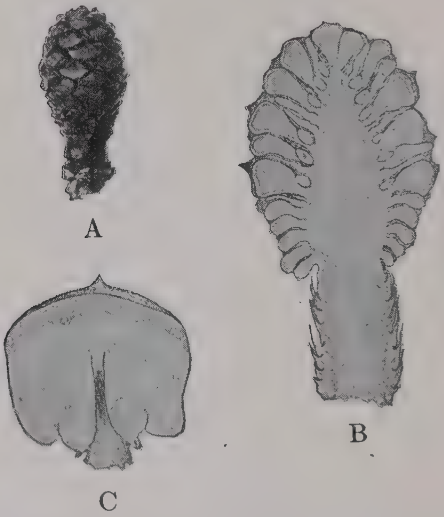

FIG. 278.—*Pinus nigra.* A, the year-old cone, natural size. B, median longitudinal section of the same cone enlarged, showing the attachment of the megasporophylls and the position of the ovules. C, an adaxial (upper) view of a megasporophyll; the outline of the wings of the future seeds are now visible.

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* In these pages *up* means in the direction of the micropyle, while *down* is the opposite direction, or toward the base of the nucellus.

that develops inside the megaspore is the *megagametophyte*, or *endosperm.*

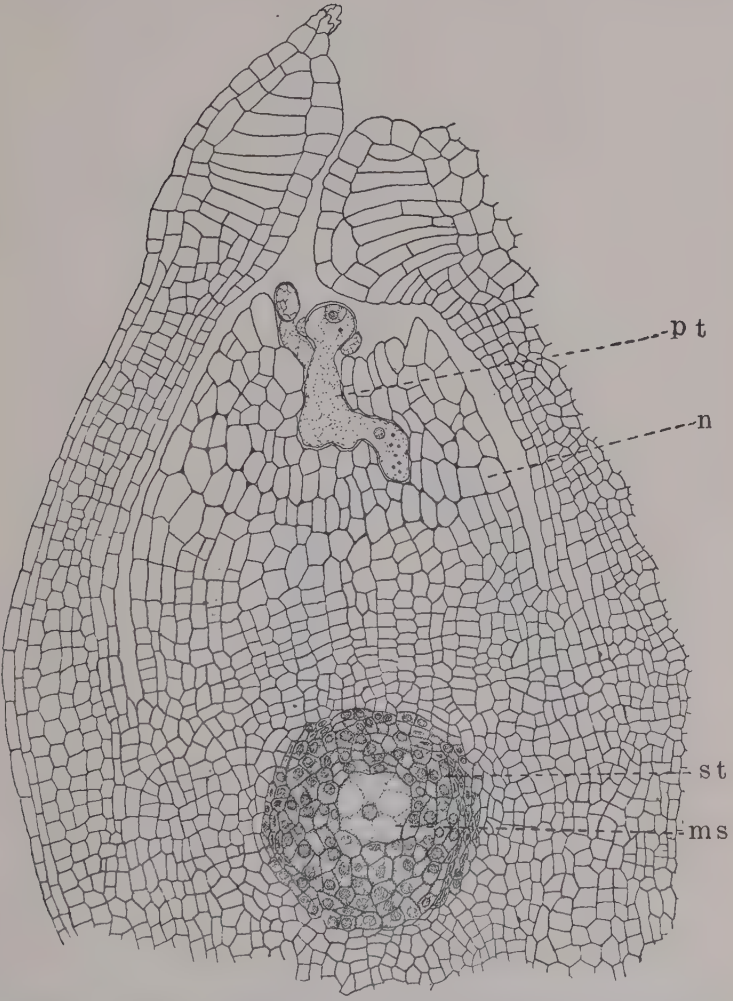

FIG. 279.—Pinus. Longitudinal section of one-year-old ovule. *pt*, pollen tube; *n*, nucellus; *ms*, megaspore; *st*, nutritive spongy tissue.

Development of the Ovule during the Second Season. In the spring of the second year, the ovulate cone and ovules begin a rapid growth resulting, in a few weeks, in a cone seven or eight centimeters in length with the functioning ovules almost as large as the mature seed.

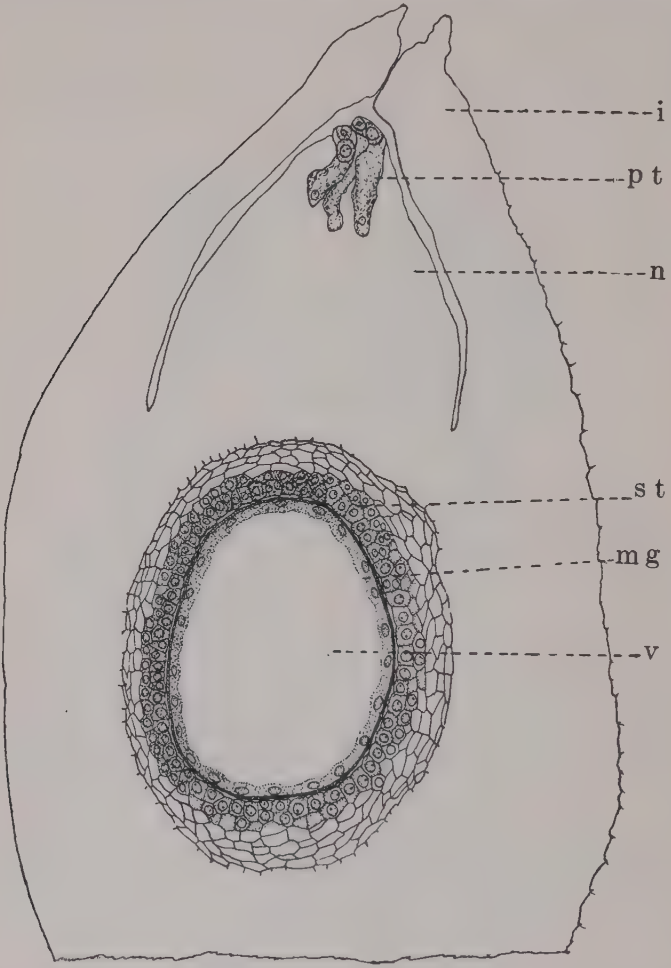

Fig. 280.—Pinus. Longitudinal section of an ovule shortly after the beginning of rapid growth in the second year. *i*, integument; *pt*, pollen tubes; *n*, tip of nucellus free from integument; *st*, spongy tissue; *mg*, megagametophyte; *v*, vacuole.

The period of rapid increase in size in *Pinus nigra* extends from about April 20 to June 1 in central Indiana. The cone increases in size from that of Fig. 278, A, to that of Fig. 270, A.

Fig. 280 is a longitudinal section of an ovule a short time after the rapid growth begins. The megaspore has increased greatly in size, chiefly as a result of hydration. In it is a large central vacuole (*v*). The cytoplasm (*mg*) is distributed in a thin, uniform layer along the periphery of the spore. In it are evenly spaced the numerous nuclei that have resulted from successive nuclear divisions. In this peripheral layer, cell formation now begins and proceeds regularly in a centripetal direction, with the result that the entire cavity of the megaspore is filled with the cellular tissue of the developing endosperm.

As referred to in a preceding paragraph, the nucellus and integument increase in size along with the megaspore and all other parts of the cone. The entire endosperm is oval or cylindrical, with rounded ends (Fig. 281, *mg*). At the end near the micropyle several archegonia (*ar*) are developed, each from a single cell.

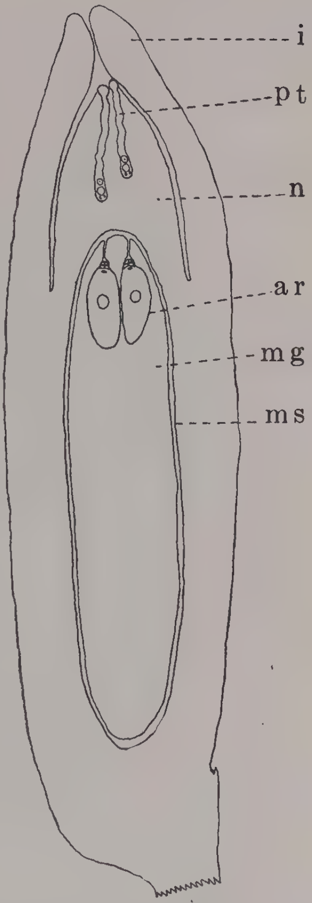

Fig. 281.—*Pinus nigra.* Outline drawing of a longitudinal section of an ovule a short time before fecundation; *i*, integument; *pt*, pollen tubes; *n*, nucellus; *ar*, archegonia; *mg*, endosperm; *ms*, megaspore membrane.

The mature archegonium consists of a small neck of about eight cells, arranged in two tiers of four cells each, a very large egg, and a very small, and often poorly developed, lens-shaped ventral canal cell just below the neck (Fig. 282). The egg and ventral canal cells were formed by the division of the large cell, the central cell.

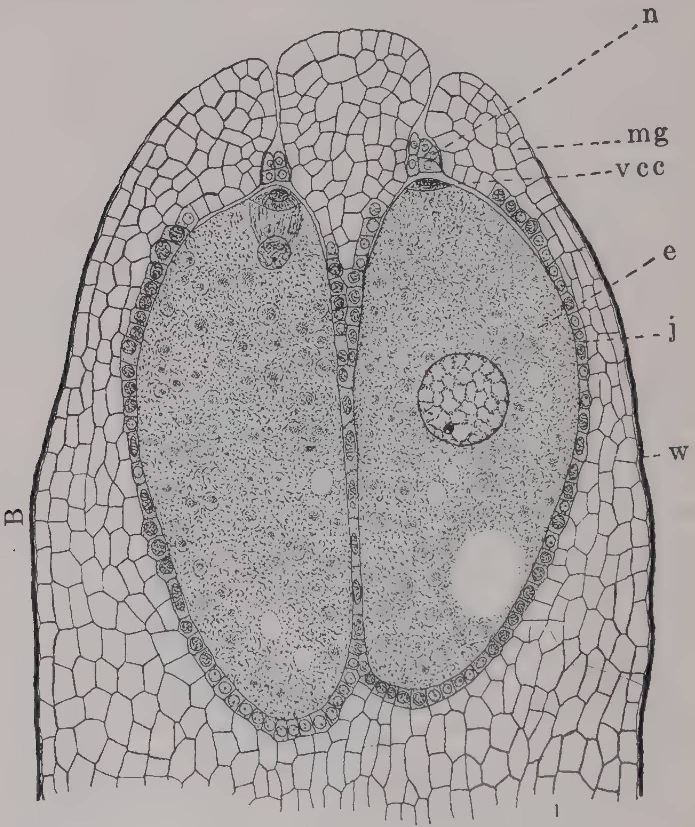

Fig. 282.—*Pinus nigra.* Longitudinal section of the upper end of the endosperm, showing two archegonia. The one at the right is mature and ready for fecundation; that at the left is younger; the ventral canal cell is being cut off.

The layer of regular cells with dense contents (*j*), surrounding the egg, constitute the jacket, or mantle. These cells contribute nourishment to the egg, their function being of the nature of a tapetum.

As the archegonia develop, the endosperm tissue grows up beyond them, and consequently a narrow passage, or canal, leads down to each archegonium (Fig. 282).

When the pine archegonium is compared with that of the ordinary fern it is seen that this organ in the pine has a greatly reduced neck, which doubtless has no function. The neck canal cell is absent, and the ventral canal cell is evanescent or may not be completely organized. The archegonium of the pine, in the poorly developed neck, the loss of a neck canal cell, and the reduced ventral canal cell, represents one of the best illustrations of regressive evolution among reproductive organs in the plant kingdom. Evolution through loss of parts (failure to develop) is further illustrated in one of the highest gymnosperms, to be mentioned later, namely, Gnetum, in which no archegonium is formed. The surviving remnant is an egg nucleus, or perhaps a poorly differentiated cell.

During the growth of the pollen tube through the nucellus in the second season the following development takes place within it: The antheridial cell divides into a stalk cell and a body cell (Fig. 283, *st*, *b*). The body cell enlarges, and both move from the cavity of the spore down into the growing end of the tube. The stalk cell remains the same or tends to disintegrate. The nucleus of the body cell divides to form two sperm nuclei. The body cell itself does not divide in *Pinus nigra* (Fig. 283, B). Since it is not surrounded by a cell wall, but by a plasma membrane only, the outline of the body cell is not always clearly discernible. The mature microgametophyte consists, therefore, of the pollen tube, in which are the two sperm nuclei, the tube nucleus, and the remains of the stalk cell.

It must not be forgotten that the pollen tube, with its contents, and the endosperm are the two gametophytes, namely, the microgametophyte and megagametophyte.

Each is a distinct individual, but living parasitically within the tissues of the nucellus. They are the haploid individuals. The megasporangium, consequently, supplies food for both gametophytes.

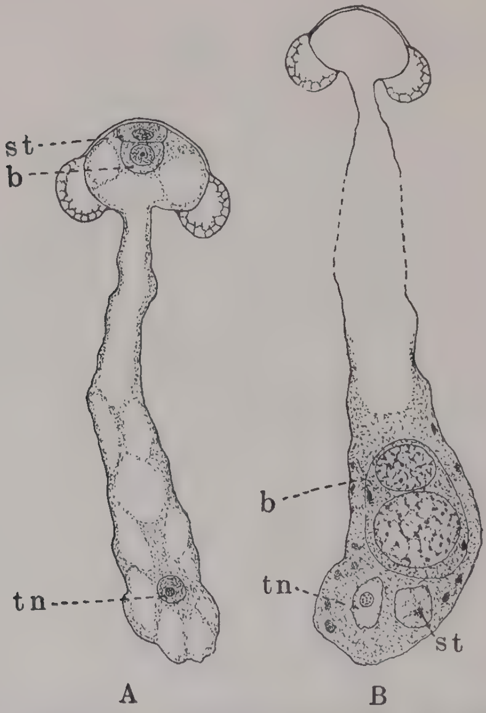

FIG. 283.—*Pinus nigra*. Two microgametophytes, pollen tubes, in different stages of development. A, the antheridial cell has divided into the stalk cell, *st*, and the body cell, *b*; *tn*, tube nucleus. B, the proximal and distal ends are shown. The proximal end is empty. In the distal end are the large body cell, *b*, with the two sperm nuclei, the stalk cell, *st*, and the tube nucleus, *tn*.

Fecundation and Development of the Embryo.—The distal end of the pollen tube continues growth down through the nucellus and the upper part of the endosperm until it reaches the egg. When in contact with the egg an opening is dissolved in the end of the tube through the action of an enzyme, and the contents are discharged into the cytoplasm. One sperm nucleus, the larger, which is usually nearer the end of the tube, functions, while all the rest of the contents is digested as food. The functional sperm nucleus passes to the nucleus of the egg, and both unite as the first nuclear division of the zygote takes place (Fig. 284).*

Following the first nuclear division in the zygote, the two resulting daughter nuclei divide in a very short time. The four free nuclei pass to the bottom of the zygote (the end farther from the micropyle) and lie in a horizontal plane (Fig. 285, *pn*). These four nuclei divide, and cell division follows, so that two tiers of four cells each are formed, the upper tier of cells being open at the upper side. These eight cells now divide transversely, and four tiers of four cells each, sixteen in all, result. This structure is known as the proembryo.

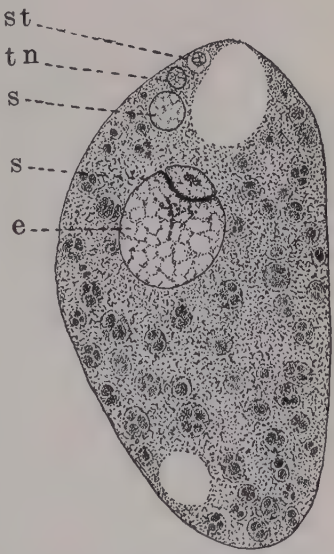

FIG. 284.—*Pinus nigra.* A stage in fecundation. *e*, nucleus of egg; *s*, functioning sperm nucleus; *s′*, second sperm nucleus; *tn*, tube nucleus; *st*, stalk cell.

The lowest tier consists of the embryonal cells (*ec*), the next tier above, the suspensor (*s*), and the third tier becomes the rosette (*r*). The tier of cells open above toward the cytoplasm of the zygote, tend to become disorganized.

In the endosperm, just below the archegonia, a narrow, cone-shaped cavity is formed by autodigestion. This cavity is the embryonal path.

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* The details of this process are too complicated to be given here.

The suspensor cells now rapidly elongate, pushing the embryonal cells down toward the center of the endosperm (Fig. 285). As the suspensor elongates its cells and the four embryonal cells separate, and each embryonal cell begins development into an embryo

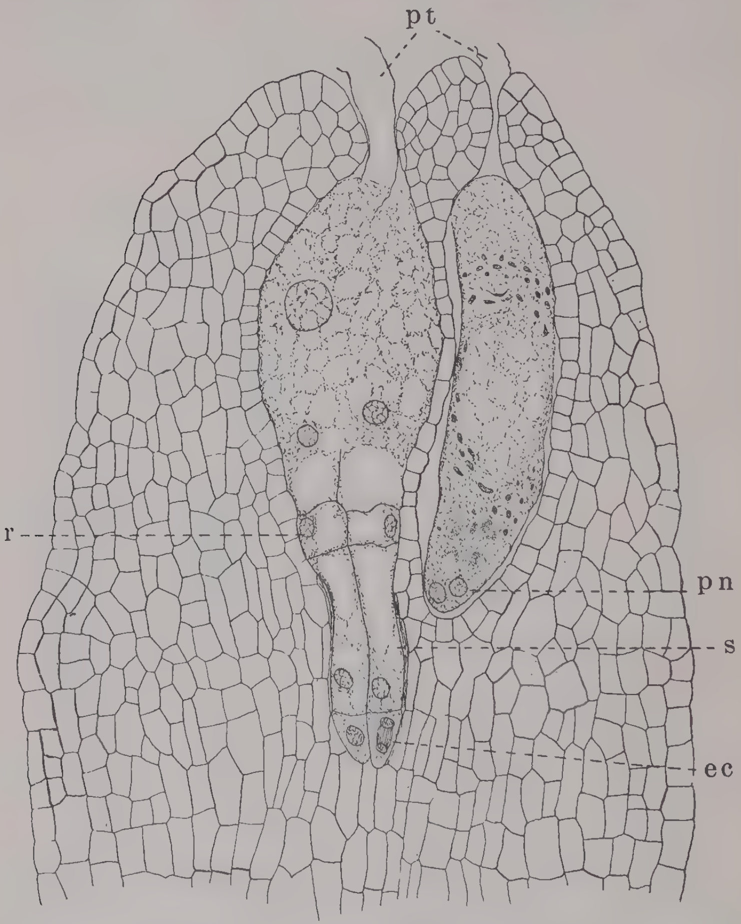

Fig. 285.—*Tsuga canadensis.* Longitudinal section of the upper end of the endosperm, showing two zygotes with proembryos in different stages of development. In the zygote at the right the proembryo consists of four nuclei at the bottom, two, *pn*, being shown. In the zygote at the left the proembryonal cells, *ec*, the suspensor, *s*, the rosette, *r*, and four cells above open on the side next to the cavity of the zygote; *pt*, remains of pollen tube.

sporophyte, i.e., an embryo pine tree. Fig. 286 is a proembryo dissected out of the endosp. Termhe long suspensor cells, now much curved, have separated, freeing the four embryonal cells, which have given rise to the four young embryos, e^1, e^2, e^3, and e^4. From every fecundated egg in Pinus, therefore, at least four embryos begin development. In some cases embryos may also begin to develop from the rosette.

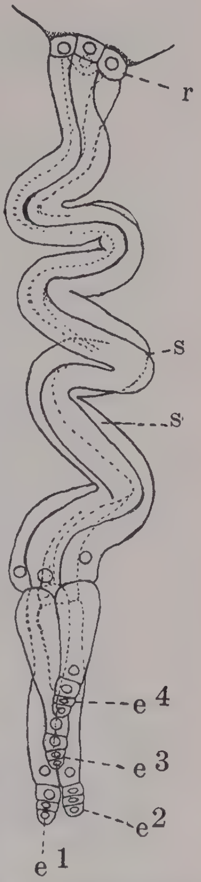

FIG. 286.—*Pinus nigra.* Proembryo dissected out of the endosperm. The separation of the suspensor cells has isolated the four potential embryos, e^1, e^2, e^3, and e^4. (From Buchholz.)

It frequently happens that two or more eggs are fecundated, and, as a consequence, many embryos may begin development in the ovule. Owing to competition among them, only one, as a rule, survives to the maturity of the seed. In some cases two embryos develop in a seed, one being usually a little larger than the other. In *Pinus edulis*, four or five embryos of varying sizes have been found in one seed.

In many gymnosperms the embryonal cells do not separate, and only one embryo develops from one fertilized egg.

Maturing Cone and Seed.—During the remainder of the summer following fecundation, the embryo gradually develops to that of the mature seed, as shown in Fig. 271, A. The endosperm also increases in size, consuming all the nucellus except a small, cap-like remnant at the micropylar end. The larger outer part of the integument becomes stony tissue. An inner and softer layer of the integument becomes the thin, separable, papery, brown membrane surrounding the endosperm.

A thin layer of tissue splits off the upper face of the ovuliferous scale to form the wing of the seed. The ovuliferous scales become brown, dry, and bony. The entire vegetative part of the cone now represents dead tissue, the embryo and endosperm being the only living parts.

Germination of the Seed.—Pine seeds may germinate readily the spring following their liberation from the cone, and many retain their viability for a number of years. Supplied with the necessary conditions of warmth, moisture, and air, the seeds will absorb water, and the embryo will begin growth. The swelling of endosperm and embryo bursts the seed coat. The hypocotyl elongates and pushes out through the seed coat, bending if necessary so that the root which develops may grow downwards.

The cotyledons, which digest and absorb the endosperm, gradually enlarge and emerge from the seed coat. By the time the endosperm is all consumed, the embryo has freed itself completely from the seed coat, and germination is at an end. The cotyledons persist for some time and function as foliage leaves until secondary leaves are developed. In some pines the embryo becomes green before it emerges from the seed; that is, chlorophyll will develop here in darkness.

The Foliage Leaf.—In many conifers the foliage leaves are inserted singly on the shoot, but in the pines they are borne in groups, or fascicles, on dwarf shoots of limited growth. The two needles in each cluster, in *Pinus nigra*, are semicylindrical in form, with the flat surfaces facing each other. Longitudinal rows of minute whitish dots indicate the position of stomata.

In a cross section is seen a central vascular region (stele) surrounded by a definite layer of cells, the sheath (Fig. 287, B). In this region are two vascular bundles, the xylem of each facing the flat (adaxial) side of the

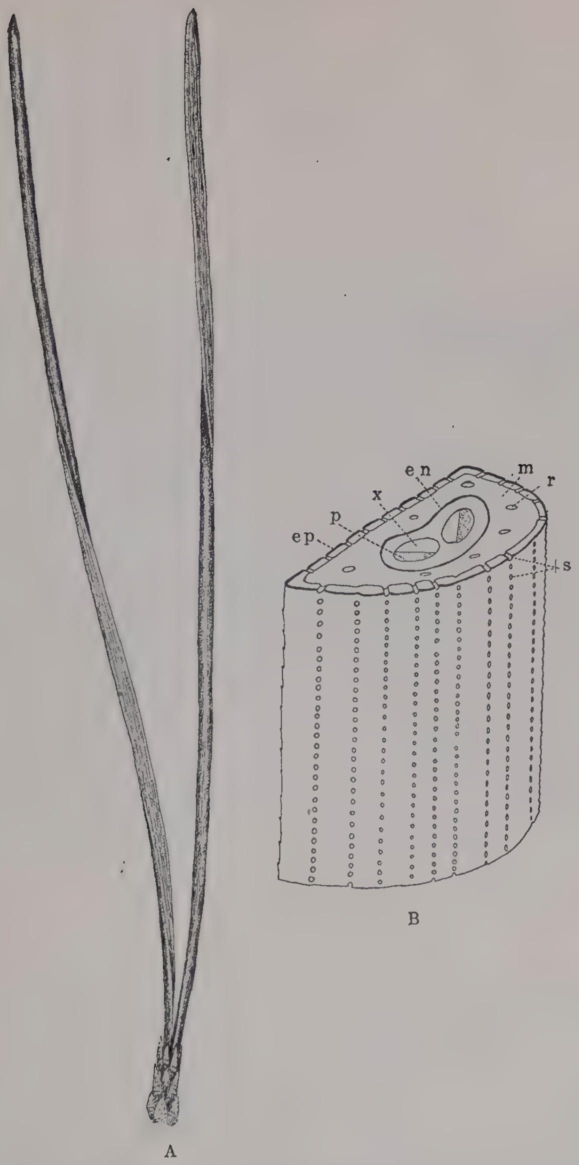

FIG. 287.—*Pinus nigra.* A, dwarf shoot bearing two foliage leaves ("needles"). B, portion of a leaf, enlarged, the cross section shown in diagram. *ep*, epidermis; *p*, phloem; *x*, xylem; *en*, endodermis; *m*, mesophyll; *r*, resin duct; *s*, stomata.

leaf. Surrounding the central region is the green mesophyll, whose cells have peculiar infoldings on their walls, thus increasing the surface over which the chloroplasts are distributed. Many intercellular spaces are present (Fig. 288). In the mesophyll are resin ducts, each surrounded by a layer of resin-secreting cells, and these in turn surrounded by a layer of thick-walled cells. The epidermal cells are thick-walled, the outer walls possessing a thick outer layer of cutin. The stomata lie at the bottom of depressions, and below each stoma is a large intercellular space. Below the epidermis is a region of cells with very thick, silvery white walls, whose cavities are connected by narrow pits (canaliculi).

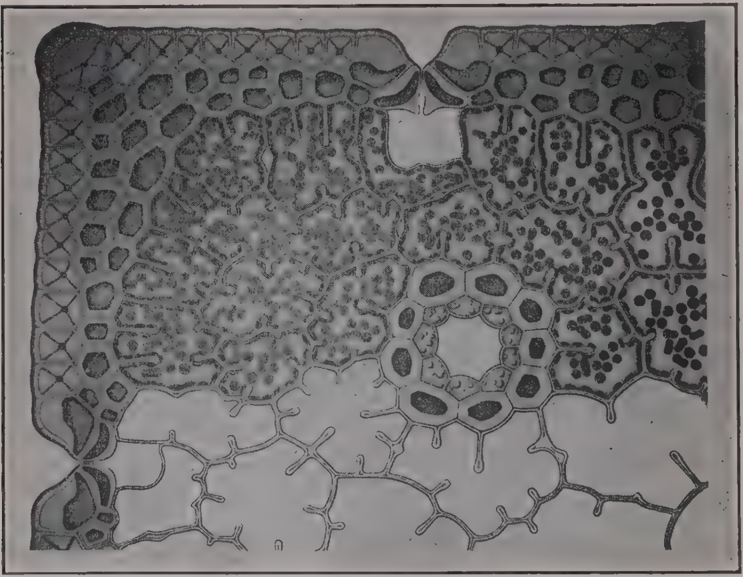

FIG. 288.—Cross section through corner of a foliage leaf, or needle, of Pine. (From Kny's Chart.)

Classification of Gymnosperms

All gymnosperms known to botanical science, both living and extinct, are included in seven great groups: (1) Cycadofilicales, (2) Bennettitales, (3) Cycadales, (4) Cordaitales, (5) Ginkgoales, (6) Coniferales, and (7) Gnetales.

1. *Cycadofilicales.*—The Cycadofilicales, sometimes referred to as the seed-bearing ferns, have no living representatives. Our knowledge of the group is based upon fossil remains found only in the Paleozoic, chiefly in the Pennsylvanian deposits. The coal measure deposits are rich in the remains of fern-like plants, which constituted about one-half of the vegetation of that time.

The sporophyte was strikingly fern-like, including not merely the usual fern habit, but also climbers and tree-like ferns. The seeds were borne at the margin of the foliage leaves, although in certain forms these differed somewhat from the purely vegetative leaves (Fig. 289). In such cases the seeds terminated naked branches and were often surrounded by a husk-like cover or cup. The microsporangia were similar to those in ferns. In general the ovules resembled those of the pines. It is doubtful whether pollen tubes were developed from the microspores. Surrounding the tip of the nucellus was a circle of cavities capable of holding water, in which the microspores were deposited at the time of pollination. The microgametophyte may have borne some resemblance to that of such water ferns as Salvinia or Azolla. In all probability motile sperms were present, swimming into the egg after the disorganization of the nucellar tissue above the archegonia.

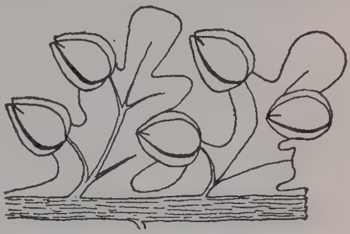

Fig. 289.—*Pecopteris pluckeneti.* Two pinnules of leaf, bearing seeds at ends of veins. (From Zeiller, after Grand'Eury.)

2. *Bennettitales.*—This extinct group, usually referred to as the fossil cycads, flourished during the Mesozoic, or age of Cycads. They were abundant during Jurassic time, numerous remains having been found in Maryland, South Dakota, and other parts of northern North America, as well as in Europe and Asia.

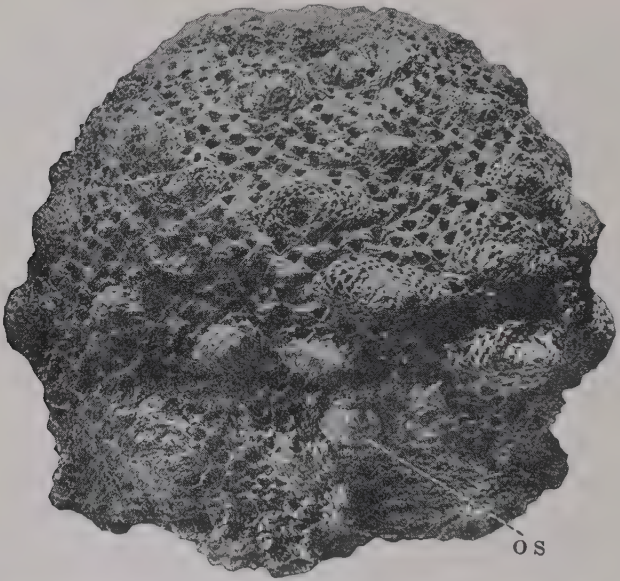

Fig. 290.—*Cycadoidea dacotensis.* Fossilized stem, or trunk; *os*, ovulate strobilus. (From Wieland.)

The stem of the sporophyte was usually a short, stocky, or tuberous body, resembling the stem of certain living cycads (Fig. 290). It bore a crown of large fern-like leaves. The stem was covered with an armor of leaf bases, from among which sprang short axillary branches bearing terminal strobili (Fig. 290, *os*). The strobili were bisporangiate, a condition rarely occurring among living gymnosperms. When the strobili were expanded at the time of shedding the pollen, they bore some resemblance to the flower of higher plants (Figs. 291, 292).

The megasporophylls were borne on an axis resembling the conical mass of carpels in a Magnolia blossom. The compound microsporophylls bore a striking resemblance to the leaves of certain ferns and produced numerous synangia.

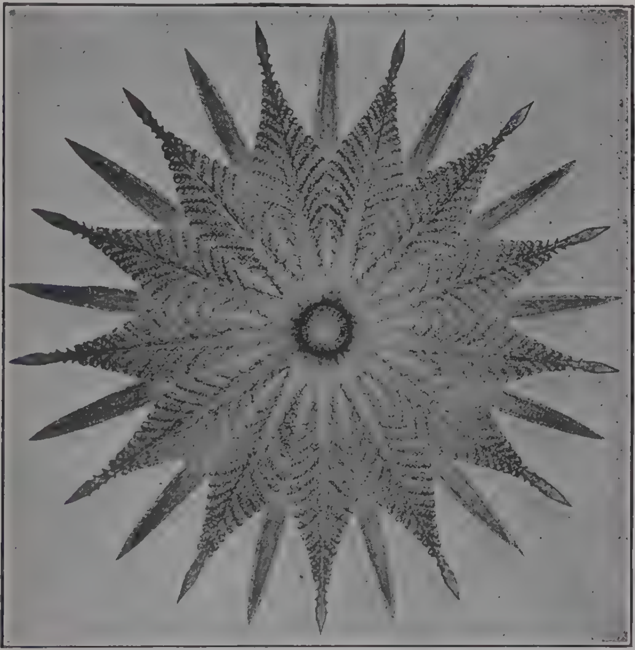

FIG. 291.—*Cycadoidea ingens.* Diagrammatic restoration of an expanded bisporangiate strobilus as if pressed out flat. The central part is the conical aggregate of carpels. Inserted below this is the circle of microsporophylls resembling fern leaves and bearing many synangia (sporangia grown together). (From Wieland.)

3. *Cycadales.*—The living cycads are confined to tropical or sub-tropical regions. About 100 species have been listed. Of the nine genera, Cycas and Zamia are most commonly encountered, species of the latter being native to southern Florida.

The columnar stem of Cycas bears a crown of large, leathery, pinnate leaves at the top, which alternate in

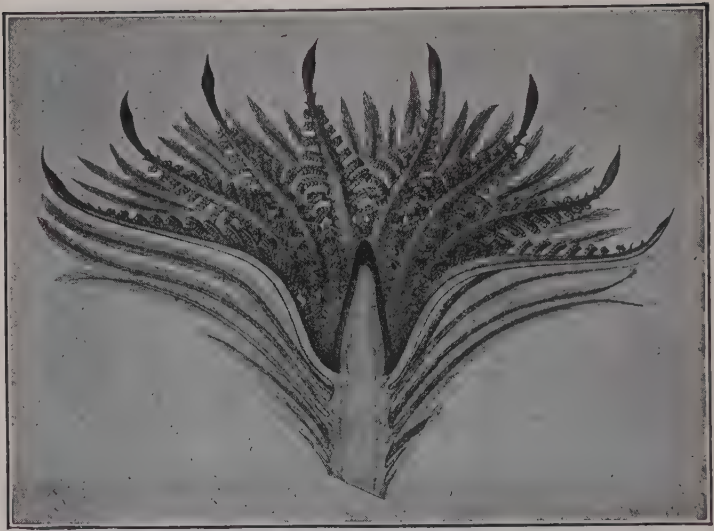

Fig. 292.—*Cycadeoidea ingens.* Restoration of an expanded strobilus in median longitudinal section. (From Wieland.)

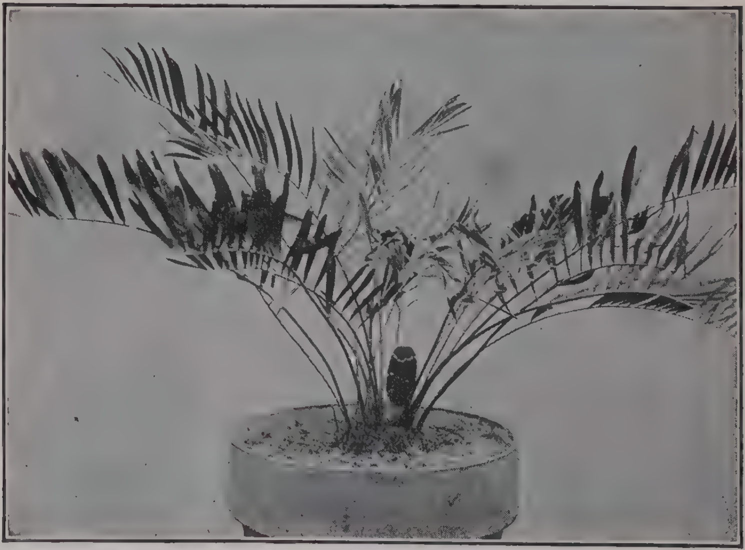

Fig. 293.—*Zamia floridana.* A pot-grown specimen with ovulate cone ready for pollination.

order of development with a crown of short scale leaves covered by a felt of brown hairs; that is, a crown of foliage leaves will be followed in development by a crown of scale leaves. The tuberous stem of Zamia, which is mostly subterranean, bears also a crown of similar foliage leaves (Figs. 293, 294).

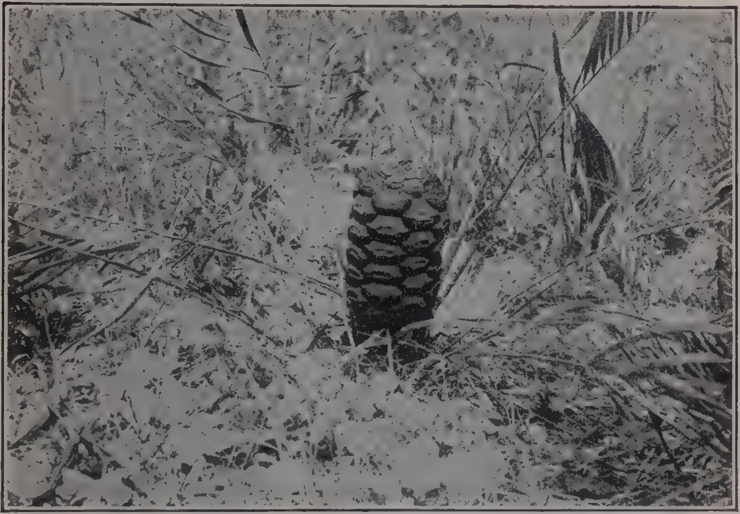

FIG. 294.—*Zamia floridana.* Fruiting plant in its native habitat near Homestead, Florida. As the seeds mature, the foliage leaves tend to die. (Photo, by P. Weatherwax.)

Staminate Strobilus.—The staminate and ovulate strobili of Zamia are quite similar in external appearance. Each microsporophyll bears two groups of microsporangia on the abaxial side (Fig. 295, A). Each megasporophyll bears two megasporangia (Fig. 295, B).

The staminate strobilus of Cycas is a large, compact, structure, bearing numerous long, epaulette-like sporophylls, which bear numerous sporangia on the lower side.

Ovulate Strobilus.—The ovulate cone of Cycas is not a compact strobilus, but a loose rosette of megasporophylls resembling reduced foliage leaves covered with a felt of stiff brown hairs. The ovules are borne on the lower pinnae, two or more on each side. The ovules seem to replace the pinnae completely (Fig. 296).

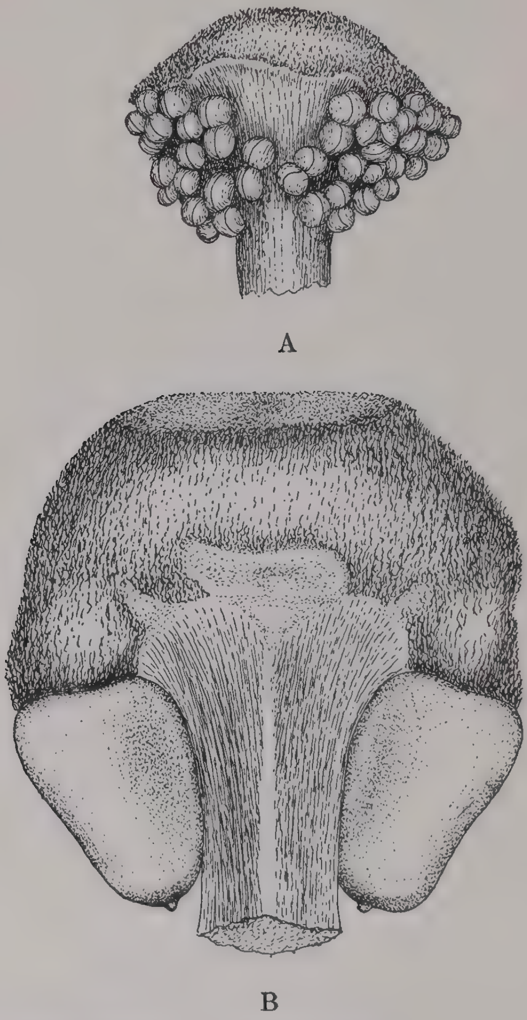

Fig. 295.—*Zamia floridana.* A, microsporophyll seen from abaxial side. B, megasporophyll.

Motile sperms are developed in the pollen tube of the Cycadales. The basal end instead of the tip of the tube grows towards the archegonium and discharges the sperms above the neck of the archegonium in a depression at the micropylar end of the endosperm. The distal end of the pollen tube, which takes in general a transverse direction in the nucellus, acts as a haustorium, or food absorber, while in the pine the distal end of the tube carries the sperm nuclei to the egg.

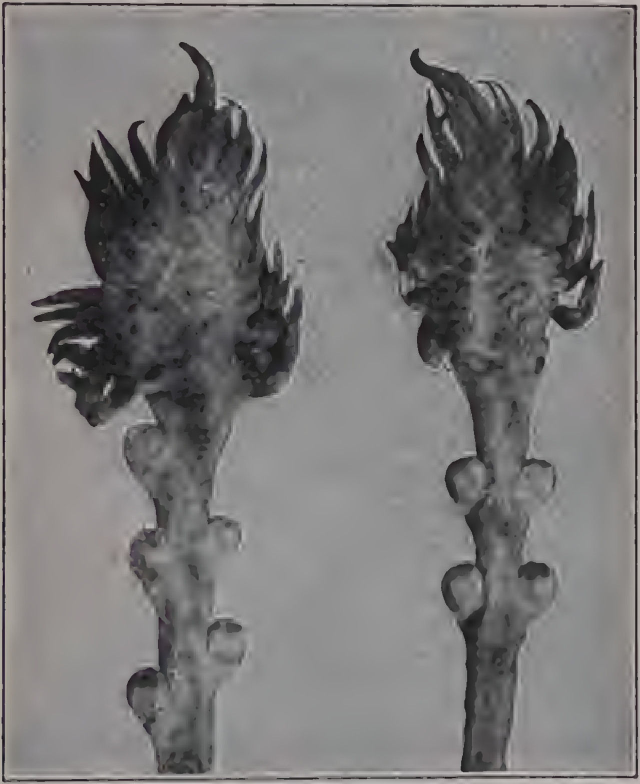

FIG. 296.—*Cycas revoluta.* Two megasporophylls. Note the pinnate character of the ends of the sporophylls.

In the mature seed of Cycas, Zamia, and other genera the external part of the integument develops into a soft, pulpy, orange-colored layer, while the inner part becomes stony.

4. *Cordaitales.*—Like the Cycadofilicales and Bennettitales, the Cordaitales represent an extinct group of gymnosperms. Their fossil remains occur in the Paleozoic deposits, and it is possible that they constituted the dominant forest type of gymnosperms at that time.

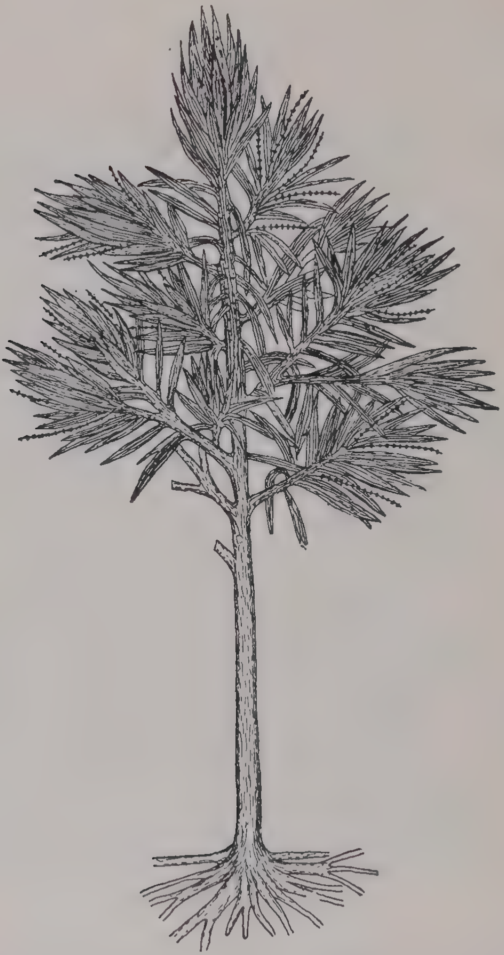

Fig. 297.—Dorycordaites. Restoration (reduced) of a tree, showing roots, trunk, and crown of branches bearing large lanceolate leaves and inflorescence. (From Grand'Eury.)

They occurred side by side with the Cycadofilicales as far back as the records go. Intergrading forms seem to indicate that the Cordaitales probably arose from the Cycadofilicales at a very early period.

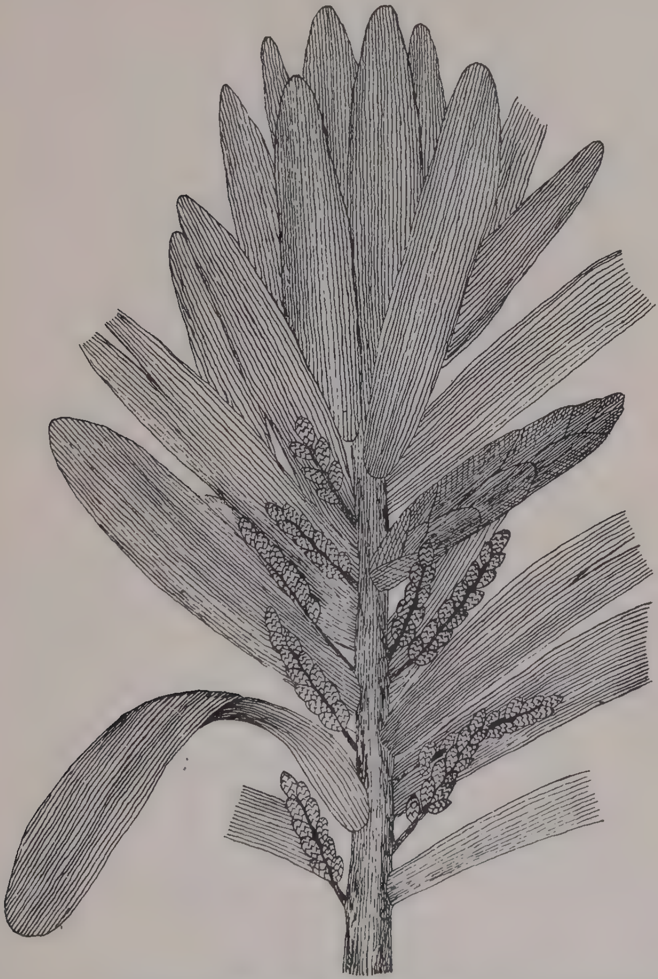

FIG. 298.—*Cordaites laevis.* Restoration of branch with spatulate leaves, and bearing numerous strobili; a large bud is seen at the right. (Adapted from Grand'Eury.)

They were tall, slender trees, often attaining a height of 30 meters, bearing a crown of large, simple, and rather broad leaves. A restoration is shown in Fig. 297.

The flowers, which occur in catkin-like clusters on lateral branches, are small and monosporangiate, as is the case of the Coniferales (Fig. 298). Both kinds are borne on the same tree, hence the sporophyte is monoecious.

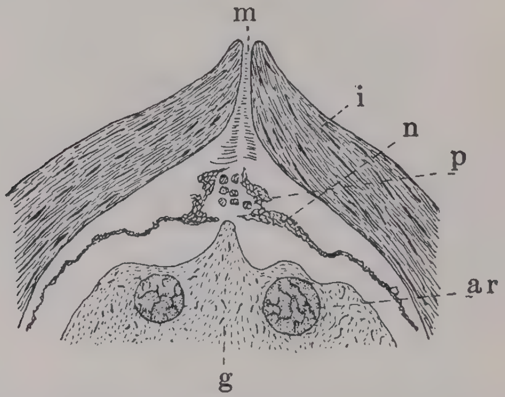

Fig. 299.—*Cycadinocarpus angustodunensis.* Longitudinal section of upper part of ovule. *i*, integument; *m*, micropyle; *p*, microspores; *g*, megametophyte; *ar*, archegonium. (From Renault.)

The staminate catkin consists of spirally arranged bracts, between which the stamens are inserted. Each stamen consists of a filament bearing three or more terminal pollen sacs. The ovulate catkin is similar to the staminate. The ovule bears a striking resemblance to that of Ginkgo (Fig. 299). Pollen grains are preserved in large quantities. Each seems to have contained a group of internal cells. Motile sperms were probably present, but it is doubtful whether a pollen tube was developed as in living gymnosperms.

Neither in the Cordaitales nor in the Cycadofilicales have embryos been found in the remains of the seeds.

5. *Ginkgoales.*—This group is represented by one living species, *Ginkgo biloba*, commonly known as the

Ginkgo tree, or maidenhair tree. Its ancestry has been traced back to the Cordaitales. The Ginkgoales were

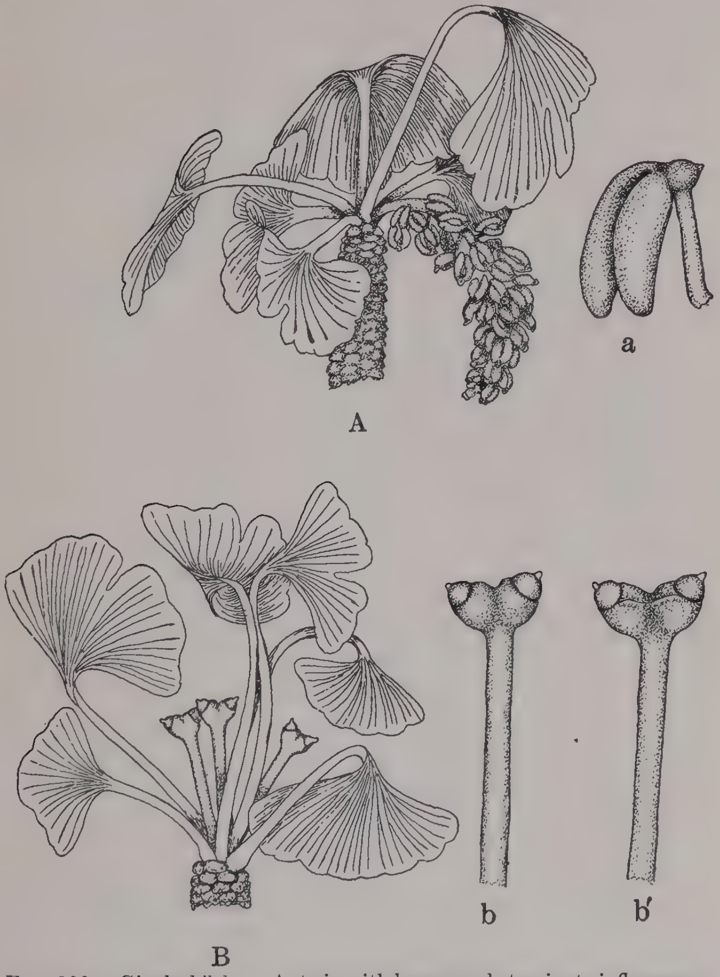

FIG. 300.—*Gingko biloba.* A, twig with leaves and staminate inflorescence; *a*, one microsporophyll. B, twig with leaves and ovulate inflorescence; *b*, megasporophyll with two ovules, seen from the under side; *b′*, the same as seen from the upper side.

probably abundant in the Mesozoic. The tree, whose leaves resemble the leaflets of the maidenhair fern

(Fig. 300), is now extensively cultivated, since it thrives well in temperate regions.

For many years it has been extensively cultivated by the Chinese and Japanese, especially in their temple grounds. For a long time it was supposed that the tree did not exist in the wild state. In recent years specimens have been reported as growing wild in the mountains of western China.

The Staminate Flowers.—Opinions differ as to whether the flowers of Ginkgo are to be regarded as strobili or merely as sporophylls of a more primitive character. The staminate and ovulate flowers occur on different trees, hence the sporophyte is dioecious. The staminate flowers are catkin-like structures borne at the ends of short branches (Fig. 300). Each stamen consists of a very short stalk from near the end of which two (sometimes more) pendent, sack-like sporangia are borne (A, *a*).

The Ovulate Flowers.—The ovulate flowers are borne also at the ends of short branches. Each flower consists of a long, slender stalk, near whose tip, as a rule, two megasporangia are borne (B, *b*, *b′*). One of these usually matures. At the base of each ovule is a little collar.

The ovule is similar in structure to that of Zamia. The distal end of the pollen tube, as in the Cycadales, becomes a haustorium, while the two motile sperms are developed in the basal end, which grows towards the archegonium and discharges the sperms.

The seeds, as they hang on the tree, resemble small plums (Fig. 301). The seed coat, as in the Cycadales, has an outer pulpy layer and an inner stony layer. The embryo has two cotyledons, one of which may be lobed.

6. *Coniferales.*—This is the largest group of gymnosperms, including the vast majority of commonly known evergreens, such as pines, spruces, junipers, firs, hem-

locks, arbor-vitae, cedars, Sequoias, yews, tamaracks (larches), bald cypress, etc.

Two large families are recognized, the Taxaceae and the Pinaceae.

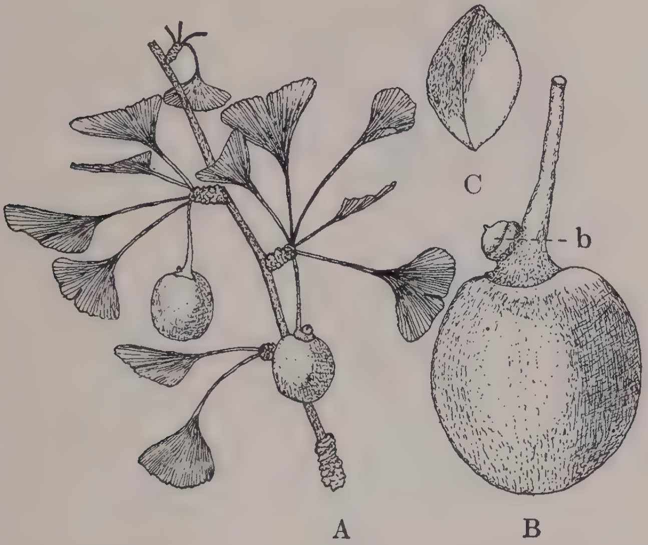

Fig. 301.—*Gingko biloba.* A, portion of branch with two mature seeds. B, mature seed, natural size; *b*, aborted ovule. C, seed, with pulp removed. (After Bailey.)

Taxaceae.—The Taxaceae, in general, have fleshy coated seeds and freely exposed ovules. There are about 11 genera and 100 species. Taxus, the yew tree, and Podocarpus are representative genera.

Pinaceae.—The Pinaceae have, in general, dry seeds borne in woody cones, as in Pinus and others.

The "cedar berry" of the red cedar, or juniper, represents a very small transformed cone, the carpels of which have grown together to form a thin pulp surrounding the bony seed or seeds.

The Pinaceae comprise 29 genera and 250 species.

7. *Gnetales.*—The Gnetales, the most highly developed of the gymnosperms, are confined to tropical or subtropi-

cal regions, although a number of species occur in the temperate zone. They are of special interest because of the resemblance of many of them to the angiosperms, both in habit and anatomical structure, and in the flowers (strobili), which suggest strongly the inflorescence of certain dicotyledonous plants. Three genera are recognized: Ephedra, Welwitschia (Tumboa), and Gnetum.

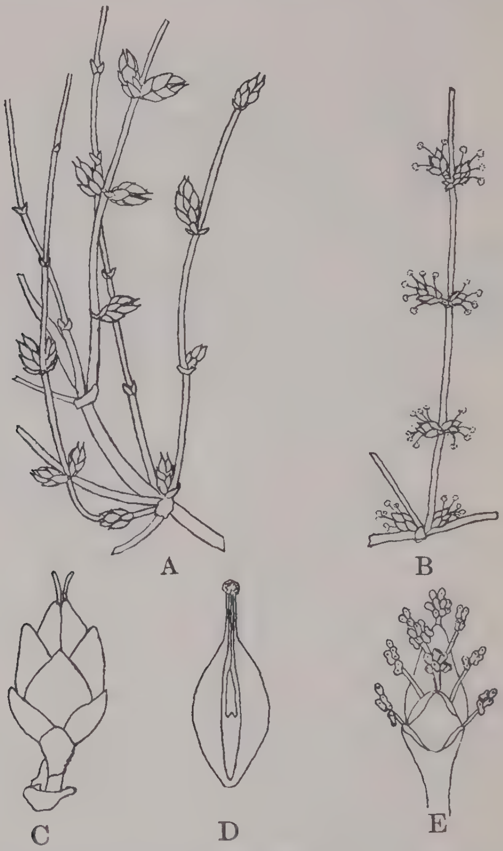

Fig. 302.—Ephedra. A, branches with ovulate strobili. B, branches with staminate strobili. C, ovulate strobilus. D, an ovulate flower. E, staminate strobilus with staminate flowers in the axils of bracts. (From Watson.)

Ephedra.—This genus includes about 50 species. In a species found in Arizona the sporophyte is a switch-like plant, with long, jointed, green, fluted stems. At each joint two scale-like leaves are borne (Fig. 302). The strobili are borne at the nodes and resemble the inflorescences of certain angiosperms.

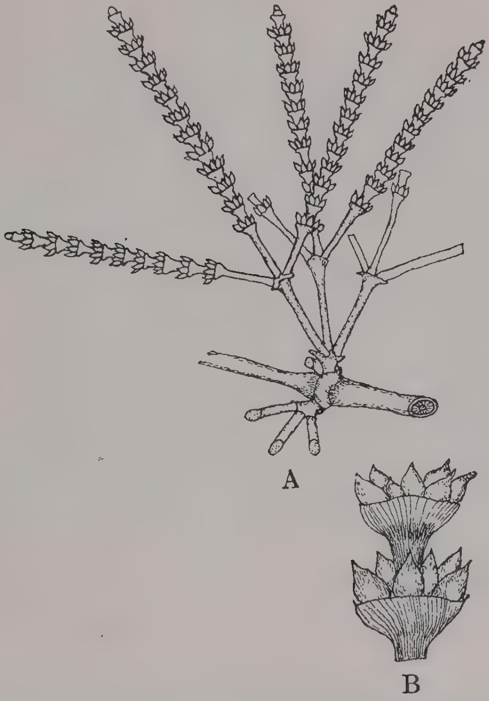

FIG. 303.—*Gnetum latifolium.* A, branches bearing ovulate strobili. B, part of ovulate strobilus. (From Blume.)

Staminate Strobilus.—A staminate "flower" consists of an axis bearing at its top two or more sporangia (Fig. 302, E). These flowers arise in the axils of the bracts of the strobilus.

Ovulate Strobilus.—The ovulate strobilus is similar to the staminate. The ovule has two so-called integuments, as in Gnetum and Welwitschia, the inner forming a long, tube-like micropyle (D). The megagametophyte (endosperm) corresponds to the usual gymnospermous type, the larger part of it being formed before fecundation, and archegonia are present.

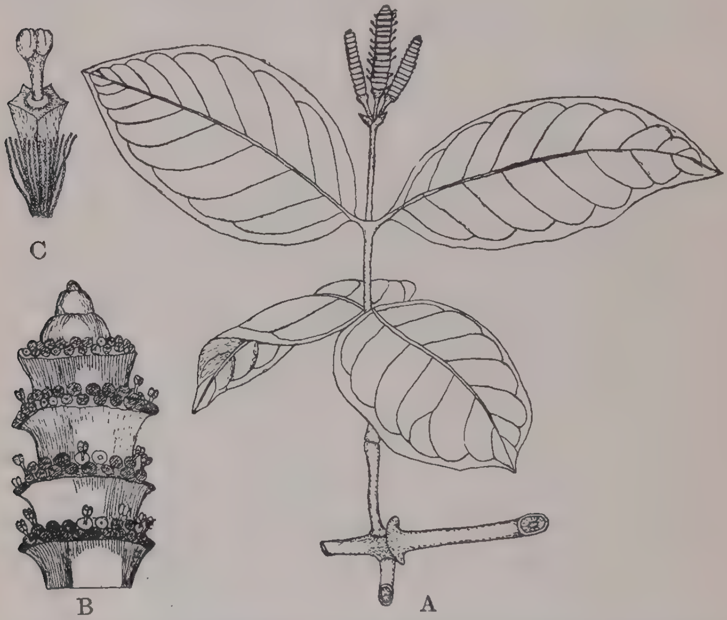

Fig. 304.—*Gnetum latifolium.* A, branch bearing staminate strobili and foliage leaves. B, portion of staminate strobilus with staminate flowers in the axils of the "connate" bracts. C, a single staminate flower. (From Blume.)

Gnetum.—In Gnetum the sporophyte may be a small tree or a woody climber. The leathery, opposite, net-veined leaves resemble those of certain dicotyledonous angiosperms (Fig. 303).

Staminate Strobilus.—In the staminate strobilus the connate bracts, in whose axils the "flowers" are borne, form a series of contiguous, but not overlapping, cups placed one above another on the axis (B). Each staminate flower consists of an axis bearing two microsporangia (in *Gnetum latifolium*) at its upper end (C).

This axis is surrounded at its base by a tube of coalesced bracts which form a sort of perianth, a structure resembling in some respects a calyx.

Ovulate Flowers.—The ovulate strobili have the same general make-up as the staminate (Fig. 304). The ovule has two integuments, and it is surrounded by a kind of perianth similar to that of the staminate flower.

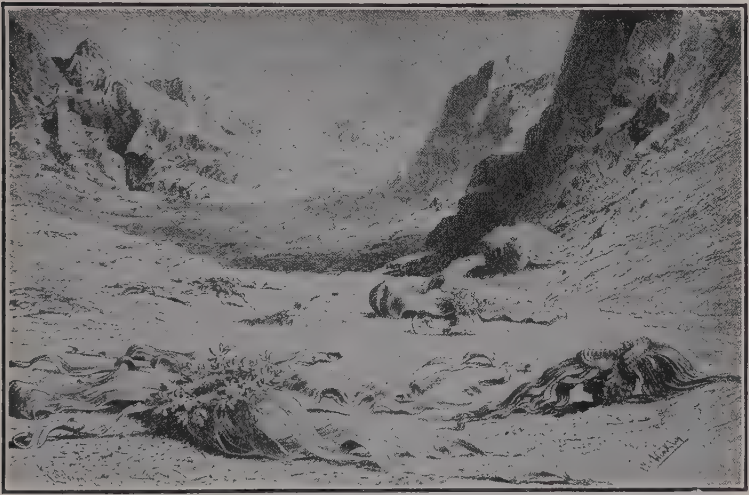

FIG. 305.—*Welwitschia mirabilis* in its natural surroundings (from a sketch by its discoverer). From Natural History of Plants by Kerner and Oliver.

In the development of the seed, Gnetum differs widely from the gymnospermous type in two very important ways, namely, in the absence of archegonia and in the development of the bulk of the endosperm after fecundation. At the time of fecundation the endosperm, in some species at least, consists merely of a layer of cytoplasm in its large upper part, in which are many free nuclei, and a small amount of cellular tissue in its lower, chalazal, end. The egg lies among the free nuclei in the upper part of the endosperm.

Welwitschia.—The sporophyte of Welwitschia has a large, woody body shaped like a turnip or sugar beet, from whose flattened crown are borne two long, straggling, strap-shaped, parallel-veined leaves. These two leaves persist throughout the life of the plant (Fig. 305). The cone-shaped strobili are borne at the edge of the crown of the stem. Only one species (*Welwitschia mirabilis*) is known. It occurs in the arid districts of western south Africa, and is one of the most remarkable plants in the vegetable kingdom.

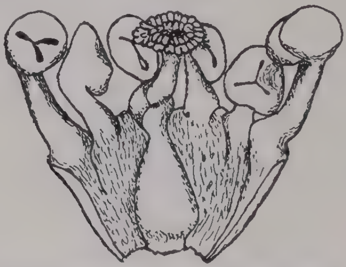

Fig. 306.—*Welwitschia mirabilis.* Staminate flower, showing six stamens united below, and a sterile ovule with twisted micropylar tube; each stamen bears three sporangia. (Adapted from Hooker.)

Staminate Strobilus.—In the staminate strobilus the "flowers" are borne in the axils of the bracts (Fig. 307, B). These differ considerably from those of Ephedra and Gnetum.

The flower consists of a circle of six stamens united at the base (monadelphous), each bearing at the upper end three sporangia (Fig. 306). Within the circle of stamens is a single terminal aborted ovule, with its long, spirally coiled micropylar tube, which ends in a broad, flaring tip.

Ovulate Strobilus.—The ovulate strobilus has the same general make-up as the staminate (Fig. 307, A). The ovule has two integuments and is surrounded by bracts resembling a perianth (Fig. 308). A set of rudimentary "stamens" doubtless appears outside the ovule.

Among fossil gymnosperms the close association of functional stamens and carpels is found only in the Bennettitales. It seems reasonable to suppose that the staminate flower of Welwitschia may have arisen through the abortion of the ovule, and the ovulate flower by the abortion of the stamens.

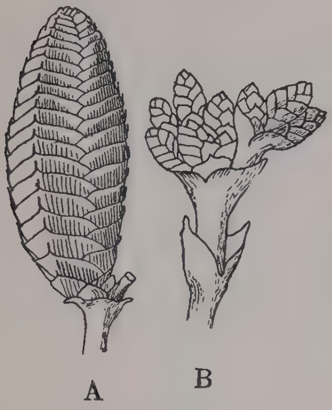

FIG. 307.

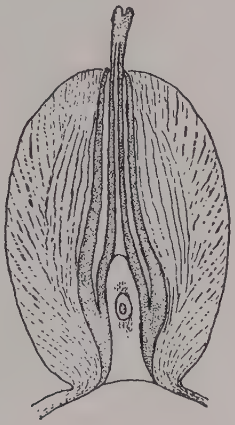

FIG. 308.

FIG. 307.—*Welwitschia mirabilis.* A, ovulate strobilus. B, staminate strobili. (From Hooker.)

FIG. 308.—*Welwitschia mirabilis.* Longitudinal section of an ovulate flower showing the surrounding winged bracts, the two integuments, and the nucellus containing the megaspore; the micropyle is formed by the inner integument. (Modified from Strasburger.)

ANGIOSPERMS

The Angiosperms, the most highly differentiated of all plants, represent the highest evolutionary development in the plant kingdom. They are grouped into two great subdivisions, the monocotyledonous and the dicotyledonous plants.

In the former subdivision the embryo has one cotyledon, while in the latter two cotyledons are present.[1]

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[1] In some monocotyledonous plants, the rudiment of a second cotyledon appears in the development of the embryo.

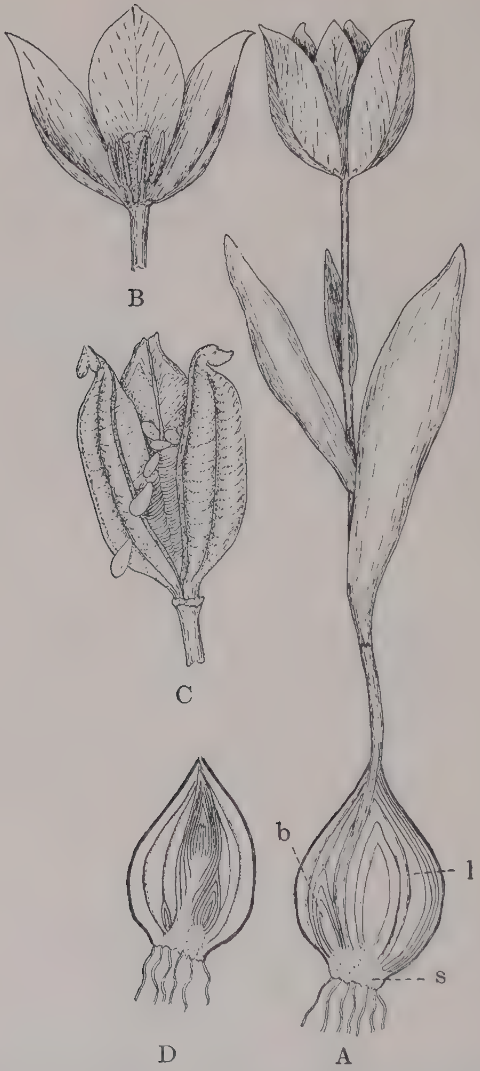

FIG. 309.—*Tulipa gesneriana.* A, habit sketch of an entire flowering specimen; the bulb in section. B, section of a flower; C, mature, dehisced fruit liberating seeds; D, longitudinal section of flowering bulb; *l*, scale leaves (leaf bases); *s*, stem; *b*, young bulb.

The Sporophyte.—The general features and external anatomy of the sporophyte may be illustrated by the common garden tulip, *Tulipa gesneriana* L., of which there are many varieties.

In a flowering specimen of the tulip, the sporophyte consists of an under ground stem, the bulb, from the center of which springs an aerial stem bearing two large and one or more smaller foliage leaves, and terminating in a single large flower (Fig. 309).

The bulb, as indicated by a longitudinal section, consists of a short, flattened, conical stem which bears roots and the fleshy, overlapping scales. These fleshy scales are modified leaf bases. Near the base of the aerial stem may be present the primordium of a bud of the following year's growth (Fig. 309, A, *b*).

The Flower.—The flower of the tulip consists of five circles or whorls of modified leaves. The six members of the two outer circles constitute the *perigone* or *perianth.* The three outer divisions of the perianth are the *calyx*, and the three inner, the *corolla.* The separate parts of the calyx are the *sepals*, and those of the corolla the *petals*. The next two circles of three members each are the six microsporophylls, *stamens.* The innermost circle of three members have developed as one piece, and constitute the *pistil.* The pistil represents, therefore, three megasporophylls, carpels. As seen externally the pistil is differentiated into three parts, *ovary*, *style*, and *stigma* (Fig. 310). In the tulip the style which is very short ends in a three-lobed stigma.

As will be seen in a cross section, the ovary contains three cavities (Fig. 310, B). In each cavity are two vertical rows of megasporangia, ovules. The place from which the ovules spring is the *placenta.* The ovary of the tulip has three placentae. Each cavity in an ovary has long been referred to as a "cell," and consequently the tulip has a three-celled ovary. Pistils, like the tulip which are composed of two or more carpels united into one piece are compound pistils. Compound pistils are recognized as having two or more placentae, two or more "cells" in the ovary or two or more styles, stigmas, or stigma lobes. A compound pistil may have but one "cell."

In many flowers as in the Larkspur and Peony the pistil is composed of one carpel. Pistils composed of a single carpel are simple pistils. A simple pistil is recognized as having one stigma, one style, one placenta and one cavity or "cell" in the ovary.

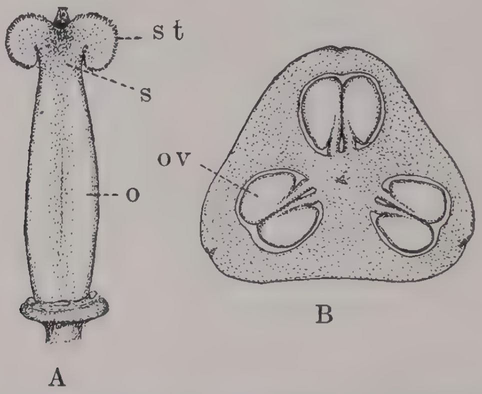

FIG. 310.—*Tulipa gesneriana.* A, pistil, somewhat enlarged; *o*, ovary; *s*, style; *st*, three-lobed stigma. B, outline of cross section of ovary, showing the three "cells," three placentae, and two rows of ovules in each cell.

In many flowers, as in the strawberry, several pistils are present.

All the stamens of a flower taken collectively constitute the *androecium;* all the pistils make up the *gynoecium.*

The Stamen.—The stamen consists of a slender stalk, the *filament*, bearing at its upper end an enlarged part the *anther* (Fig. 311, *a*, *f*). The continuation of the filament into the anther forms the *connective.* As a general rule the anther consists of four microsporangia, two on each side of the connective, although the number of sporangia in an anther in Angiosperms varies from one to several. The arrangement of the four sporangia

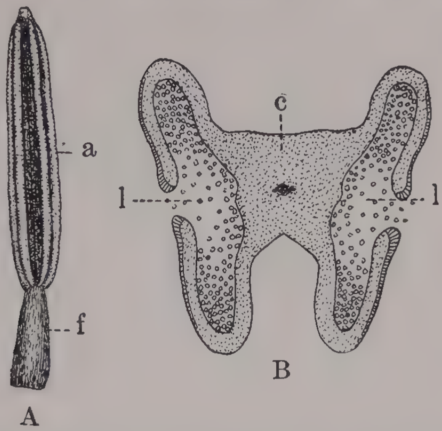

FIG. 311.—*Tulipa gesneriana.* A, an adaxial (inner) view of a stamen. B, diagrammatic outline of a cross section of the anther after dehiscence. *a*, anther; *f*, filament; *l*, loculus, or "cell" of anther; *c*, connective.

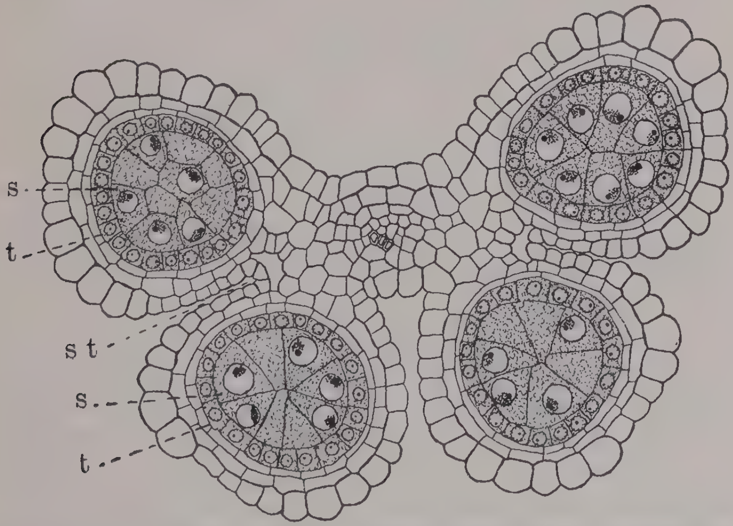

FIG. 312.—Cross section of anther of Johnson grass (*Holcus halepensis* L.) *s*, pollen mother cells; *t*, tapetum; *st*, stomium, place of dehiscence.

is made clear in a cross section of an immature anther of simple structure as shown in Fig. 312. The center of each sporangium is occupied by the microspore mother cells, *pollen mother cells* (*s*). These are surrounded by a layer of nourishing cells, the tapetum (*t*). Outside of the tapetum is the wall of the sporangium consisting of a number of layers of cells. In the tulip and lily the large cells just beneath the epidermis have characteristic band-like thickenings upon the walls. This layer is the *endothecium*, which assists mechanically in the dehiscence of the anther. Opposite the partition between each pair of sporangia, the epidermal cells become characteristically changed, and constitute the *stomium* (*st*). The stomium marks the line of opening or dehiscence, which in the tulip and lily is longitudinal. As the anther matures, the cellular partition between adjacent sporangia breaks down throwing the two cavities into one, which is known as the loculus or "cell" of the anther (Fig. 311, B).

The Pollen Spore.—The mature microspore of *Lilium candidum* will be described here. It consists of two cells, one included within the other. The large cell of the spore is the tube cell, and the smaller lenticular or crescentic cell within is the antheridial cell (designated also as the generative cell) (Fig. 332, P). The antheridial cell is delimited by a plasma membrane only. In some plants the antheridial cell divides before the pollen is shed. The wall of the pollen spore consists of two layers, the exine and intine. The exine is in the form of a beaded net which covers the intine with the exception of an elliptical area known as the germ pore. The intine is a soft thin layer rich in pectine. The pollen spores spring from pollen mother cells in the young anther. Their development will be described in a later paragraph.

The Ovule.—We may become familiar with the fully formed ovule (megasporangium) by noting the parts as seen in a longitudinal section. The plant selected as an illustration here is the dwarf Larkspur (*Delphinium tricorne*), and a longitudinal section of the ovule with its attachment to the placenta is secured by taking cross sections of the simple pistil (Fig. 313). The central and somewhat conical part of the ovule is the nucellus (*n*) surrounded by the integument (*i*). Within the nucellus is the seven-celled megagametophyte. As

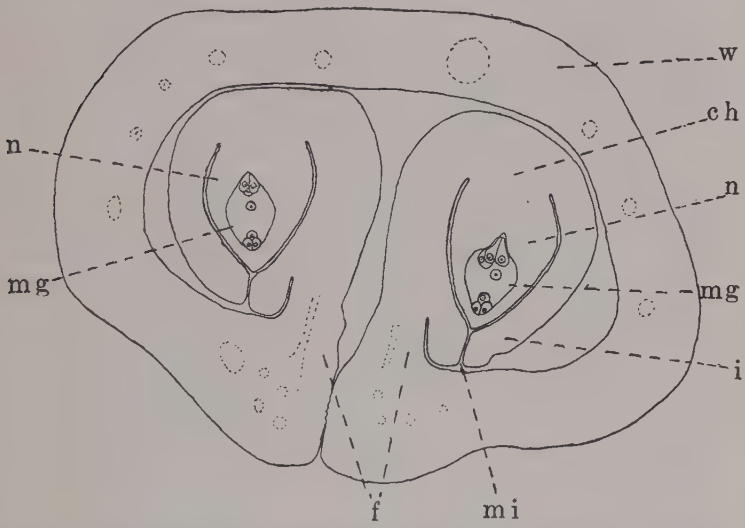

Fig. 313.—Cross section of the ovary of the dwarf Larkspur (*Delphinium tricorne*), showing two ovules cut longitudinally; *w*, wall of ovary; *n*, nucellus; *i*, integument; *mi*, micropyle; *f*, funiculus; *ch*, chalaza; *mg*, megagametophyte consisting of seven cells.

in the pine ovule the free end of the integument forms the microphyle (*mi*). The integument and nucellus which are united at the base are continued backwards into the stalk or funiculus (*f*) connecting the ovule with the placenta. In some plants the funiculus is very short, in others it is distinguishable as a little cord. The nucellus and funiculus may form a straight line, or the ovule may be folded over as in the figure, so that funiculus and integument are united laterally, and the micropyle is brought near to the placenta. At the base of the nucellus is the chalaza (*ch*).

The Megagametophyte or Embryo-sac.—As stated above, the typical megagametophyte, more commonly referred to as the embryo-sac (*mg*), consists of seven cells at the time of fecundation. The group of three cells in the micropylar end constitute the egg-apparatus; the three at the chalazal end, the antipodal cells, and the large cell between containing one or more large vacuoles is the primary endosperm cell. It is very

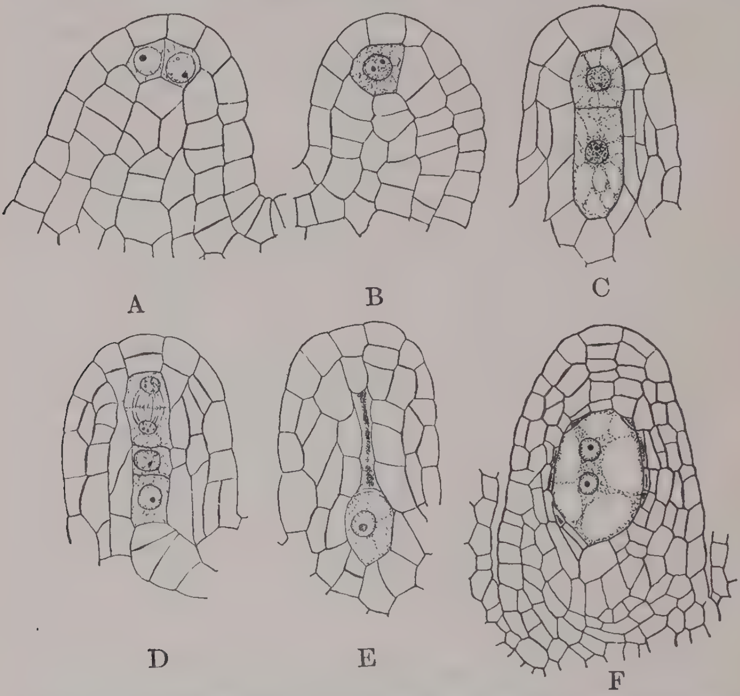

FIG. 314.—*Delphinium tricorne.* Longitudinal sections of several stages in the development of the ovule and megaspores, the nucellus only being shown. A, B, nucellus before the appearance of the integument, the megaspore mother cells shown with contents. C, megaspore mother cell has divided; D, the tetrad of four potential megaspores are present; E, the functional megaspore is germinating, and the three other megaspores above are being digested and absorbed; F, megaspore with two nuclei.

evident that the large endosperm cell makes up the bulk of the megagametophyte (Fig. 315, *ec*). In the egg-apparatus, the cell which is usually inserted more deeply, is the *egg* (*e*). It is pear shaped, and may be recognized by the fact that the nucleus and cytoplasm lie in the lower and larger end, while the upper end is occupied by a vacuole. In the other two cells of the egg apparatus, the *synergids* (*s*), the nuclei and cytoplasm lie in the upper ends of the cells and the vacuoles in the lower ends. In the Larkspur the three antipodal cells (*an*) are much larger than those of the egg-apparatus and more densely filled with cytoplasm.

In the Angiosperms as a whole the antipodal cells represent a very variable group. In some plants these cells are not formed at all. In others, as in certain lilies, they may be poorly and incompletely developed, while in others they divide to form a larger mass of cells. In the latter case their role is probably that of elaborating food.

The Development of the Ovule, Megaspores, and Megagametophyte.—This seven-celled megagametophyte and the ovule will doubtless be better understood if a few steps in the development of each are followed.

In the primordium of the ovule the nucellus is the first to appear as a small protuberance upon the surface of the placenta (Fig. 314, A, B). At the base of the nucellus the integument next appears as a fold growing up around and finally covering the nucellus. A conspicuous hypodermal cell (sometimes two in this plant) is now recognized at the apex of the nucellus. This is the megaspore mother cell. With further growth, the megaspore mother cell by two successive divisions gives rise to a tetrad of four potential megaspores, arranged generally in an axial row (C, D). At this stage the integument (not shown in the figure) equals the height of the nucellus.

One of the potential megaspores, that nearer the chalaza, becomes functional, and, by further growth, enlarges and consumes the other three potential megaspores, as well as the adjacent cells of the nucellus (E). This megaspore enlarges rapidly and its nucleus divides. One daughter nucleus passes to one end of the spore and the other to the other end. A large vacuole occupies the center (F). These nuclei soon divide when two nuclei are present in each end of the spore. These

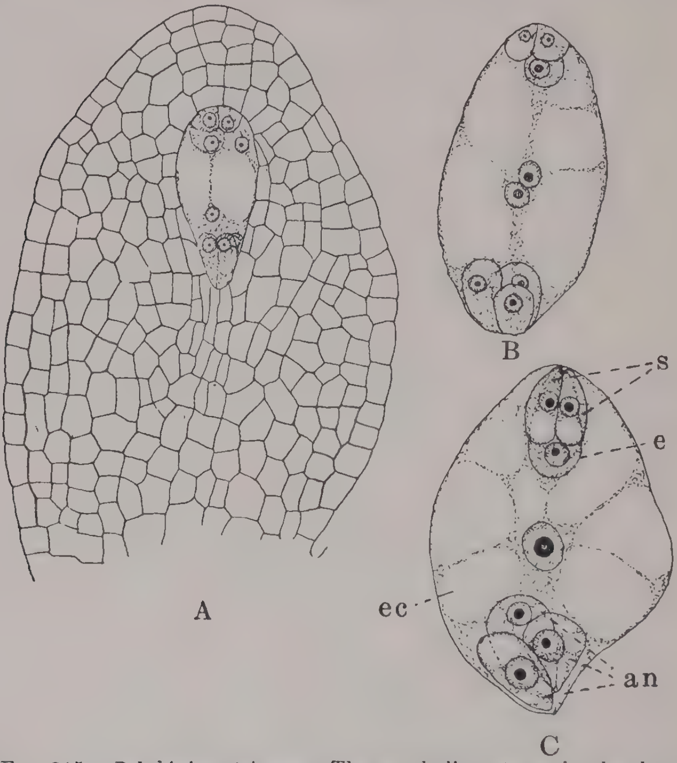

Fig. 315.—*Delphinium tricorne.* The concluding stages in the development of the ovule and megagametophyte. A, developed nucellus showing position of nearly mature megagametophyte. B, later stage; the polar nuclei are approaching each other; C, mature megagametophyte; *s*, synergids; *e*, egg; *ec*, primary endosperm cell with its large nucleus formed by the fusion of the two polar nuclei; *an*, antipodal cells.

nuclei also divide, giving rise to four in each end. Cell formation takes place, by which three cells, the egg apparatus, are formed in the micropylar end involving three of the nuclei and leaving the fourth free. In like manner the three antipodal cells are formed in the chalazal end with the fourth nucleus lying free in the cytoplasm (Fig. 315, A). The two free nuclei are termed the polar nuclei. In the vast majority of angiosperms the two polar nuclei unite before fecundation to form the nucleus of the primary endosperm cell (Fig. 315 B, C). In a number of plants, as in some species of Lilium, the polar nuclei do not unite until the time of fecundation when they fuse with the second sperm nucleus in a manner to be described in a subsequent paragraph.

The Development of the Megagametophyte in Lilium. In the foregoing we have seen that of the four megaspores produced, only one became functional, the other three being consumed. In Lilium, however, the four spores function together to form the megagametophyte. In the tetrad stage the four nuclei lie free in the megaspore mother cell, i.e., cell division does not follow by which four separate spores are formed as in Delphinium. The entire tetrad included in one cell contributes to the formation of the megagametophyte. This is made clear in Fig. 316, A to F, which represent longitudinal sections. In A the megaspore mother cell constitutes the bulk of the nucellus (*n*). The beginning of the inner integument (*i*) has appeared. An older stage (B) shows the enlarged nucellus and the two integuments, the inner (*i*) and the outer (*oi*). The micropyle is formed by the inner integument in this species. Two nuclei are now present in the megaspore mother cell. The nuclear division that gave rise to them was a reducing division. The result of the second nuclear division is shown in C. The cell and its four nuclei constitute a tetrad of megaspores, all of which as stated function in forming the megagametophyte. Two of these nuclei pass to the micropylar (upper) end of the cell and the other to the opposite or chalazal end (D). All nuclei now divide

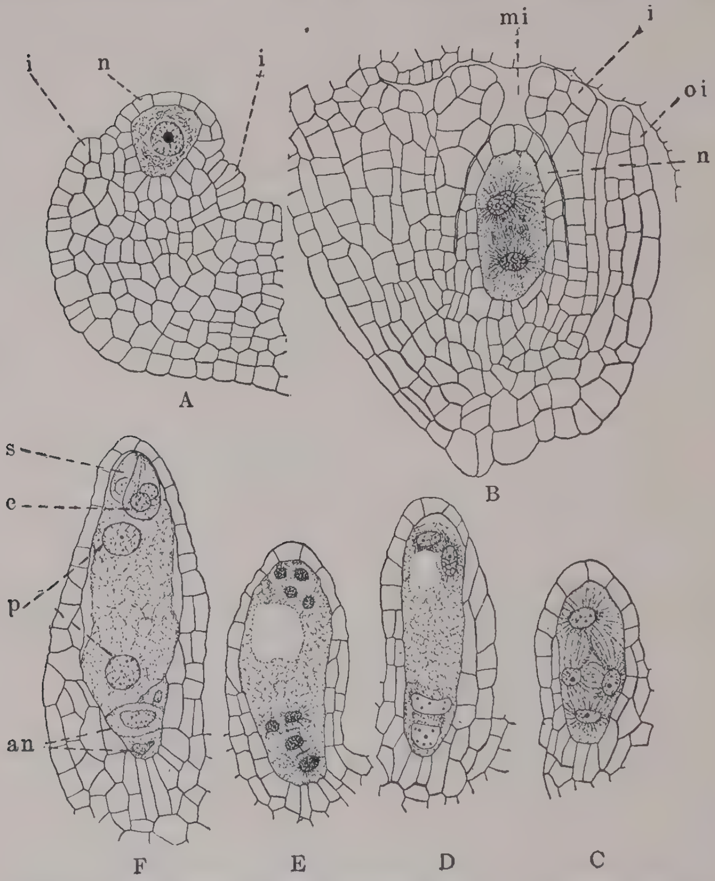

Fig. 316.—Development of megagametophyte in *Lilium candidum.* All figures are longitudinal sections. A, young ovule; the megaspore mother cell comprises the bulk of the nucellus; *i*, inner integument; B, older stage of ovule; the nucleus of the megaspore mother cell has divided; *n*, nucellus; *i* and *oi*, outer and inner integuments respectively; *mi*, micropyle; C, megaspore mother cell with four tetrad nuclei; D, two nuclei in each end of the cell; E, four nuclei in each end. F, megagametophyte ready for fecundation; *e*, egg; *s*, synergids; *p*, polar nuclei; *an*, antipodal cells.

with the result that four occupy each end of the cell (E). Cell division follows, and three cells are organized in the micropylar end to form the egg apparatus, three in the chalazal end which are the antipodal cells, while the two polar nuclei remain free in the large central cell, the primary endosperm cell. As in the Larkspur the egg apparatus consists of the egg (*e*) and two synergids (*s*). In *Lilium martagon* and *L. candidum*, the three antipodal cells are not always normally developed, and the group may soon disorganize. The polar nuclei (*p*) approach but do not fuse until the arrival of the second sperm nucleus.

In typical Angiosperms, the megagametophyte consists of the *seven-celled* structure as described in the foregoing. There are many exceptions. In some cases this structure may possess fewer cells than seven, as the antipodal cells may not be formed at all; in still other cases the antipodal cells may divide giving rise to a more massive tissue.

The Microgametophyte.—A functional pollen spore having reached the stigma, the tube cell begins growth and develops a slender tube which makes its way through the stigma and style into the ovary, and continues until its distal end reaches the egg apparatus. The tube nucleus and antheridial cell together with all the cytoplasmic contents of the pollen grain pass down into the end of the tube. The tube nucleus is always near the end of the tube and presides over its growth. The nucleus of the antheridial cell (generative cell) divides on its way down the tube unless this division has already taken place in the pollen spore. In Lilium the nucleus of the antheridial cell divides after it enters the tube.

Fecundation.—The distal end of the pollen tube grows into the egg-apparatus, destroying one or both of the synergids. The wall at the end of the tube is dissolved and the contents are discharged. The tube nucleus is no longer to be recognized. One of the sperm nuclei enters the egg and fuses with its nucleus. The other sperm nucleus is usually absorbed as food. In some plants the second sperm nucleus unites with the two polar nuclei to form the nucleus of the endosperm cell. This occurs in some species of Lilium and in a number of other plants. As stated in a preceding paragraph the

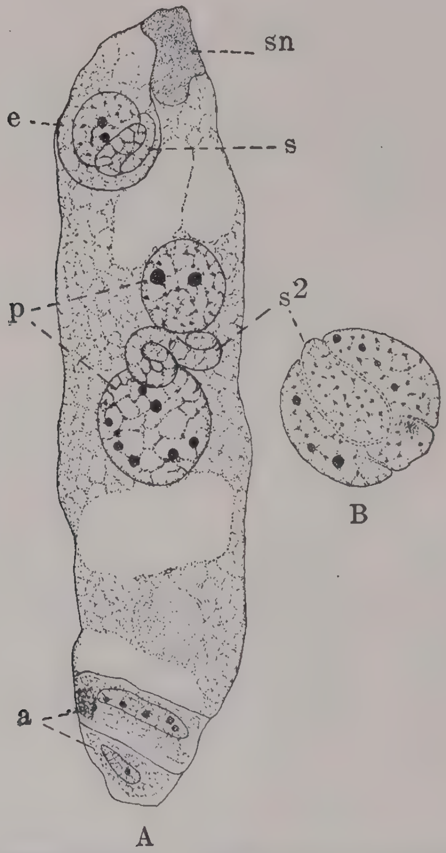

FIG. 317.—*Lilium martagon.* A, megagametophyte at the time of fecundation. *sn*, disorganized synergid; *e*, egg; *s*, sperm nucleus uniting with nucleus of the egg; s^2, second sperm nucleus uniting with polar nuclei, *p*; *an*, antipodal cells. B, the fusion of second sperm nucleus and polar nuclei almost complete.

polar nuclei in such cases do not fuse until the second sperm nucleus arrives. The fusion of the two polar nuclei and second sperm nucleus is sometimes referred to as a second fertilization, and the fusion of the two sperms with egg and polar nuclei respectively, double fertilization. The process is illustrated in Fig. 317.

The fusion of the second sperm with the polar nuclei is without significance save in a few plants. The most notable of such plants is Indian corn, *Zea Mays*, where this fusion is now acknowledged to be responsible for the phenomenon known as *xenia*, or the effect of the pollen upon the endosperm. More definitely stated xenia consists in imparting the dominant endosperm characteristics of the pollen parent to the endosperm of the seed of the ovulate parent. To illustrate, if the ovulate flowers of a sweet corn plant whose endosperm would be normally sugary if pollinized from a sweet corn parent, be pollinized with pollen of field corn whose endosperm is starchy, the result will not be sugar corn but starchy corn. Starch will prevail in the endosperm instead of sugar, the starchy characteristic being transmitted presumably by the second sperm nucleus which probably unites with the polar nuclei.

The Development of the Dicotyledonous Embryo.—Following fecundation two structures begin development from the megagametophyte, namely, the embryo from the zygote or fecundated egg, and the endosperm from the primary endosperm cell.

To illustrate very briefly the development of the embryo a few steps in the process will be presented from that of Capsella (Bursa) which is illustrated in Fig. 318.

The zygote elongates and divides transversely into a short row of cells, the proembryo (A). The terminal or distal cell of this row, that farthest from the micropyle, becomes the body of the embryo (*e*) while the others give rise to the suspensor (*s*). In the stage (A) the terminal cell is divided lengthwise. The suspensor becomes a row of about eight or ten cells. The cell nearest the micropyle (A, B, E) is greatly enlarged. By the elongation of the suspensor the body of the embryo is pushed down into the endosperm cavity. The body of the embryo enlarges, becoming globular, and by transverse and longitudinal cell divisions there result two tiers of four cells each (B, C). The terminal tier of four cells will give rise to the cotyledons and apex of the stem, the basal tier will form the hypocotyl, and from the basal end of the hypocotyl will ultimately develop the root.

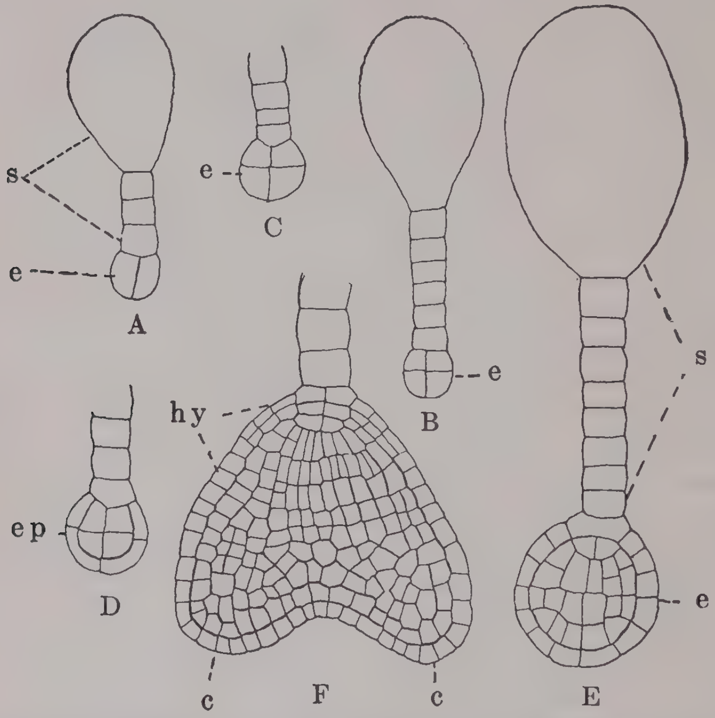

FIG. 318.—*Capsella bursa-pastoris.* Embryos in different stages of development dissected out of the ovules; *s*, suspensor; *e*, body of embryo; *ep*, epidermis; *c*, cotyledons; *hy*, hypocotyl.

The two tiers of four cells each mentioned above divide parallel with the outer surface of the embryo cutting off the layer of primary epidermal cells (D).

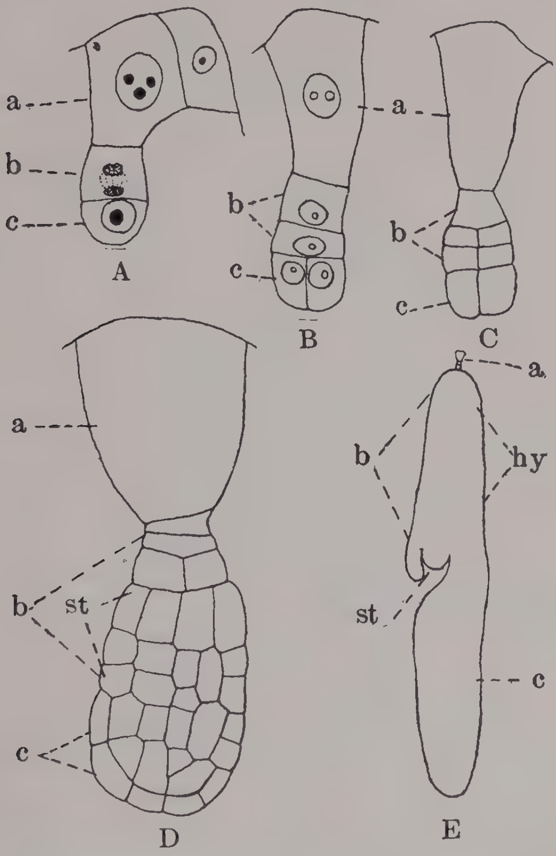

Fig. 319.—Sagittaria. Longitudinal sections of embryos in different stages of development. A, embryo, a row of three cells, *a*, *b*, and a remaining synergid. B, C, D, older stages; E, nearly mature embryo; *st*, stem apex. (A-D adapted from Schaffner.)

The body of the embryo remains globular for a time (E). Very soon, however, the distal end becomes broad and somewhat flattened. Here growth is localized at two opposite points which is manifested in the appearance of two protuberances or lobes of equal size (F, *c*). These are the primordia of the two cotyledons. Between the two cotyledons the epicotyl will develop later. Fig. 320 is a section of a young seed with small embryo in position. In Capsella the embryo grows rapidly consuming the endosperm almost as rapidly as it is formed.

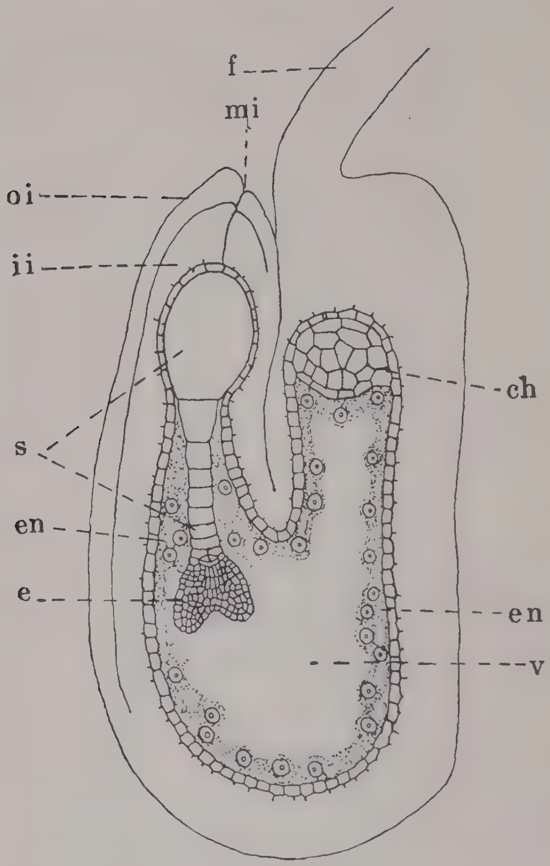

Fig. 320.—Capsella. Longitudinal section of an immature seed; *f*, funiculus; *mi*, micropyle; *ii*, and *oi*, inner and outer integuments; *ch*, chalaza; *e*, body of embryo; *s*, suspensor; *en*, endosperm; *v*, vacuole. (Adapted from Bergen and Davis' "Principles of Botany." By permission of Ginn & Company, Publishers.)

When the seed is mature a large embryo differentiated into a hypocotyl and two large cotyledons fills the cavity of the seed, no endosperm being present.

The Embryo of a Monocotyledonous Plant.—As an illustration a few earlier stages in embryo development of Sagittaria will be selected. As in the case of a dicotyledonous embryo the zygote gives rise first to a proembryo consisting of a row of cells, as shown in Fig. 319, A. The terminal cell (*c*) will give rise to the cotyledon; the middle cell (*b*) to the hypocotyl, stem tip, and some suspensor cells, while the basal cell is the large part of the suspensor. B, C, and D are successively older stages. The parts that have developed from cells *b* and *c* are indicated respectively by these letters in D. Fig. E is an outline (diagrammatic) of a longitudinal section of the nearly mature embryo. It is clear that the entire distal end of the embryo becomes the cotyledon. The tip of the stem (*st*) is seen in a depression at one side. The stem tip is partly surrounded by the baes of the cotyledon.

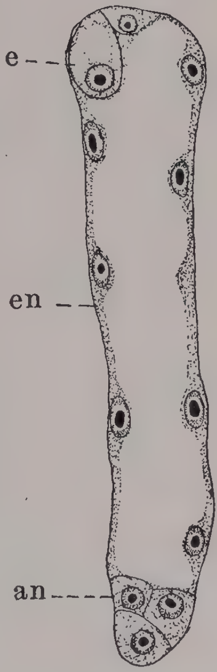

Fig. 321.—A longitudinal section of the megagametophyte a short time after fecundation. The fecundated egg, *e*, has not divided; the endosperm, *en*, consists of a parietal layer of cytoplasm with a number of free nuclei; *an*, antipodal cells.

The Development of the Megagametophyte (Endosperm) Following Fecundation.—The growth of the endosperm from the large primary endosperm cell begins simultaneously with the development of the embryo. In typical cases the ovule gradually enlarges, and the primary endosperm cell increases enormously in size by hydration. By repeated nuclear divisions there arise many free nuclei which are distributed in the parietal layer of cytoplasm, the central cavity of the primary endosperm cell being filled with cell sap (Fig. 321).

In plants like Capsella whose seeds lack endosperm when mature, very little cellular endosperm is developed. The embryo grows so fast that the endosperm is consumed almost as rapidly as it is formed. The result is as stated above a mature seed with a large embryo but no endosperm.

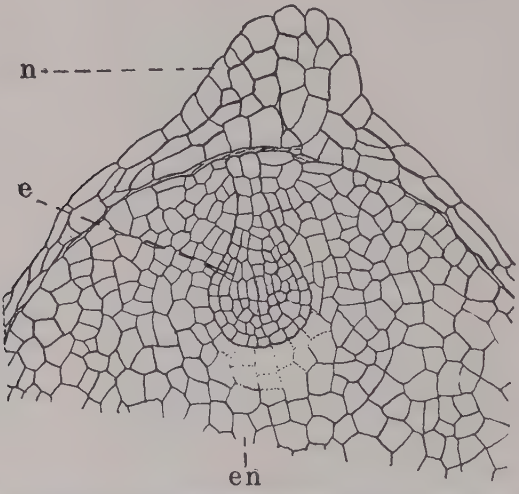

Fig. 322.—*Actea alba.* Longitudinal section of the micropylar end of an immature seed, the integument being omitted; *n*, nucellus; *e*, embryo; *en*, endosperm.

In other types of Angiosperms, however, the development of the embryo is less rapid in comparison with the growth of endosperm, and the result is a smaller embryo and a relatively large mass of endosperm (Figs. 322, 323). In such plants a large number of endosperm nuclei may be present before the zygote has undergone the first division (Fig. 321). The megagametophyte at this stage consists, therefore, of the antipodal cells (*an*) and the parietal layer of cytoplasm with a number of nuclei.

Near the embryo cell formation will begin and proceed along the periphery of the primary endosperm cavity and towards its center until the entire space is filled. Fig. 322 illustrates the micropylar end of a nearly mature seed of one of the Ranunculaceae (*Actea alba*) as seen in longitudinal section. The relatively small embryo is completely surrounded by the cellular endosperm. Fig. 323 is an outline of a section of a mature seed of the same plant.

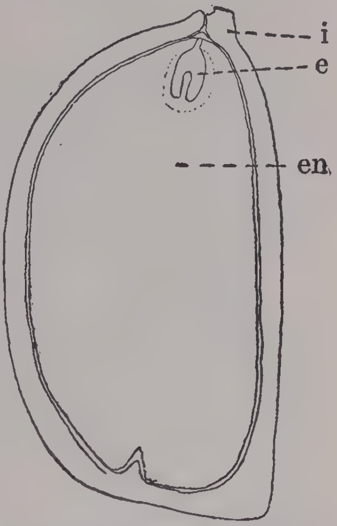

FIG 323.—*Actea alba.* Outline of a longitudinal section of a mature seed; *i*, seed coat (integument); *e*, embryo; *en*, endosperm.

The Maturing of the Seed and the Formation of the Fruit.—During the development of embryo and endosperm, changes take place in the nucellus and integuments of the ovule. In the type represented by Capsella, the nucellus is consumed at an early stage, and the integuments are changed into the seed coat, whose dead cells are crushed and flattened into the two thin layers. In some Angiosperms the large nucellus of the ovule is not consumed during seed development, but it persists and remains in the mature seed where it is known as *perisperm.* In the meanwhile, as the ovules grow and mature into seeds, the pistil enlarges also through growth and becomes transformed into the fruit. The small ovary of the tulip, for example, becomes the large capsule of the mature fruit.

The Difference between Seed Formation in Gymnosperms and Angiosperms.—When we recall the process of seed formation in Gymnosperms, it is seen that the bulk of the endosperm is developed before fecundation, whereas in the Angiosperms the endosperm is formed after fertilization. In all Gymnosperms with the exception of Gnetum, an archegonium, an organ characteristic of Bryophyta and Pteridophyta, is present, while in Angiosperms the archegonium is probably represented by the egg cell alone.

Types of Seeds.—In the foregoing pages attention was called to the development of seeds (1) in which a large embryo but no endosperm is present at maturity, and to those (2) in which a small embryo and a large mass of endosperm result.

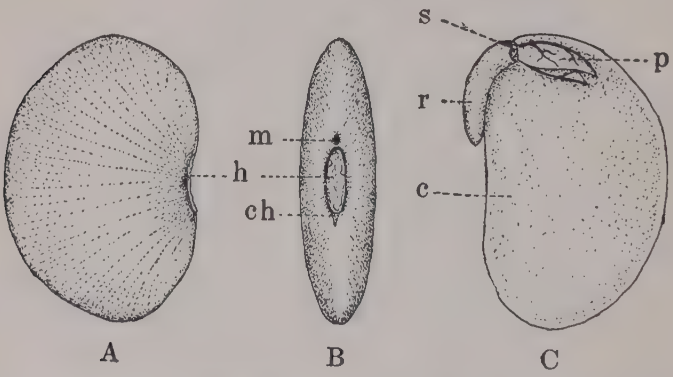

Fig. 324.—Seeds of lima bean soaked in water. A, side view; B, view from the concave edge; C, embryo with one cotyledon removed; *h*, hilum; *m*, micropyle; *ch*, chalaza; *c*, cotyledon; *r*, hypocotyl, here called the radicle; *s*, scar remaining after removal of cotyledon.

Seeds Lacking Endosperm at Maturity.—As a representative of this type of seed we may select the familiar Lima bean (*Phaseolus lunatus*).

Viewing the seed externally, we observe at the concave edge a large scar, the *hilum* (Fig. 324, A, B, *h*), indicating the place at which the seed was attached by a short cord to the pod, or fruit. Near the hilum is the *micropyle* (*m*). The seed coat is a skin-like cover consisting of two layers, which were derived from the two integuments of the ovule.

The embryo has a rather stout stem, *hypocotyl* (*r*), to which is attached at its upper end two large opposite cotyledons (*c*). The part of the stem above the cotyledons is the epicotyl which bears the first two foliage leaves in a young stage of development. Between these two leaves is the primordium of a bud. The epicotyl with its young leaves has long been referred to as the plumule. The lower, free rounded end of the hypocotyl is the beginning of the primary root.

Seeds with Endosperm.—In this type of seed the embryo is relatively small in comparison with the bulk of the seed.

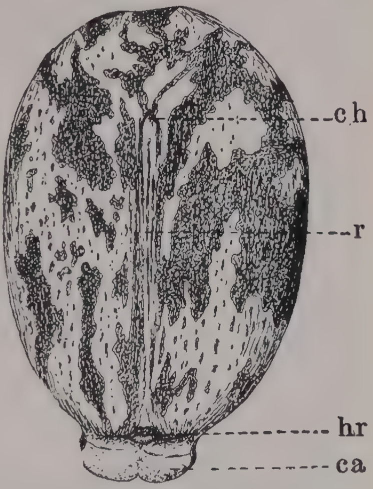

Fig. 325.—Castor oil seed (Ricinus) seen from the flat side. *ca*, caruncle; *hi*, hilum; *r*, raphe; *ch*, chalaza.

A good example is the seed of the castor oil plant (*Ricinus communis*). Here the seed coat develops into a rather firm brittle shell, testa, often revealing conspicuous color patterns (Fig. 325). At the micropylar end of the seed there is developed from the seed coat a conspicuous mass of tissue, the *aril* (*ca*), known also as the caruncle. The micropyle is located at the posterior edge of the aril on the flattened side of the seed.

The embryo has a short hypocotyl, bearing at its upper end two opposite, broad but thin cotyledons. Fig. 326, A, is a view of the seed cut in two flatwise showing the surface of one cotyledon (*c*) and the hypocotyl (*h*). Between the cotyledons is the primordium of a bud. Surrounding the embryo is the massive endosperm. In Fig. 326, B, which represents the seed cut in two longitudinally at right angles to the surface of the cotyledons, the relative size of embryo and endosperm is shown. In this and similar seeds the cotyledons digest and absorb the endosperm during germination, and also function as the first foliage leaves after germination.

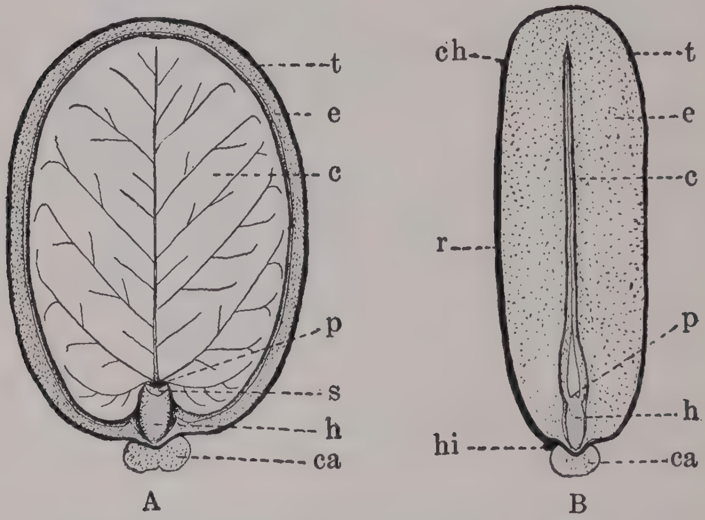

Fig. 326.—Castor oil seed (Ricinus). A, view of seed halved flatwise showing surface of cotyledon and hypocotyl. B, a longitudinal section at right angles to the surface of the cotyledons. *t*, testa; *e*, endosperm; *c*, cotyledons; *ch*, chalaza; *r*, raphe; *hi*, hilum; *ca*, caruncle or aril; *h*, hypocotyl; *p*, plumule; *s*, scar left after removal of one cotyledon.

The Seed of Indian Corn.—As another illustration of a seed with endosperm at maturity we may select the grain of Indian corn. A grain of corn is a whole, achene-like fruit known also as a *caryopsis*. As the grain matures the wall of the ovary and the integuments of the ovule become grown together and mature as a thin, skin-like layer. In a logitudinal vertical section of a grain the relation of all parts may be easily made out (Fig. 327). The embryo is situated at one side, which is marked externally by an elongated depression. The remainder of the seed is the endosperm (*e*). The embryo possesses one large cotyledon (*c*) whose infolded upper margins almost or quite enclose the epicotyl and whose lower part partly surrounds the hypocotyl. The hypocotyl is covered directly by a sheath, the *coleorhiza* (*rs*). The epicotyl bears two or more small leaves, the older folded about the next younger.

The axis of the corn embryo comprises the first two or three nodes of the plant. To the first node is attached the cotyledon.

The Aril.—The term, aril, is applied to any special, fleshy or succulent out-growth of the funiculus or seed coat. Among the common wild plants whose seeds possess conspicuous arils is the twin leaf, *Jeffersonia diphylla* (L.) Pers. The caruncle of the castor oil seed has already been mentioned. The large succulent aril covering the seed of the nutmeg constitutes mace. Sometimes the term aril is used in a very broad sense to include the hair-like outgrowth of the cotton seed, which constitutes the cotton of commerce.

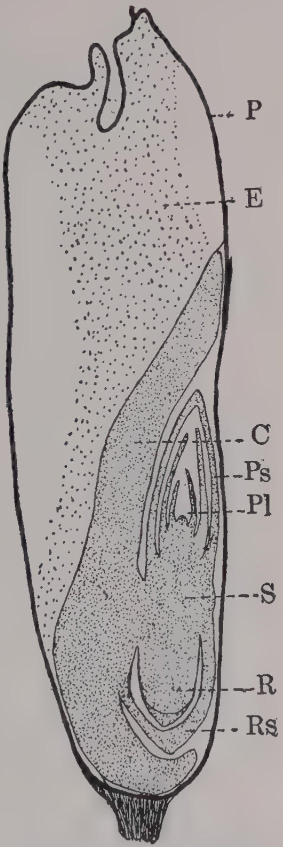

Fig. 327. Outline of longitudinal section of a grain of corn at right angles to the flat surface. *p*, pericarp; *e*, endosperm; *c*, cotyledon; *ps*, plumule sheath, coleoptile; *pl*, plumule; *r*, primordium of root; *rs*, root sheath or coleorhiza.)

Germination of the Seed and the Seedling.—One of the most fundamental characteristics of all seed-bearing plants is the fact that the embryo is capable of retaining its viability for a long period of time in the dormant state even under a very wide range of conditions of moisture and temperature. This quality of the seed has undoubtedly played a large role in enabling seed plants to acquire and maintain dominance upon the land areas of the earth. The range of viability varies from several months or a year to many years, although the upper limit is much under one hundred years. Seeds of the tobacco plant are said to retain viability for about twenty years. Many seeds of the Leguminosae also retain viability for a long while.

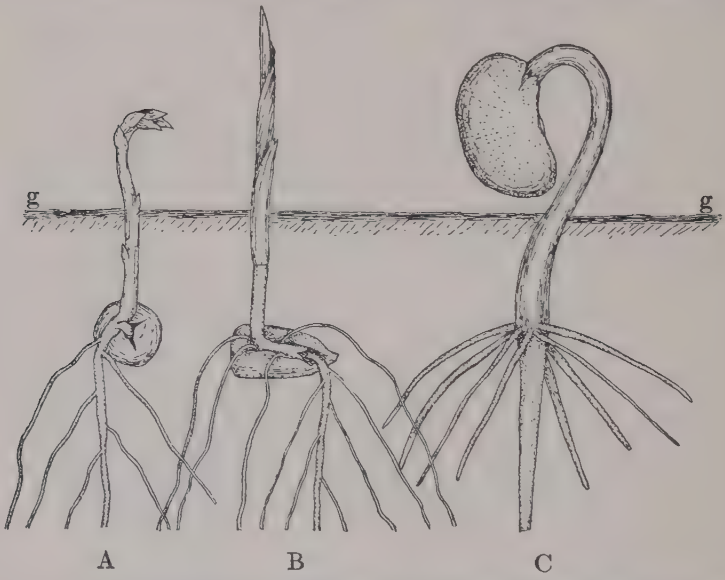

Fig. 328.—Different ways in which seedlings emerge from the soil, or come up. A, garden pea; B, corn; C, Lima bean; *g*, ground level.

Viable seeds will germinate, some immediately they are mature, others later; provided the proper conditions of moisture, warmth and oxygen are present. During germination the growing embryo has not only the task of digesting the food richly supplied in the cotyledons or in the endosperm, but it must free itself of the seed coat and emerge from a cover of soil, both processes being accomplished at the expense of much energy, and often involving a severe struggle. It sometimes happens that the embryo of certain seeds becomes severely mutilated in freeing itself from the seed coat.

The first step in germination is the absorption of water. As a result the embryo and the endosperm, if present, swell up sufficiently to burst the seed coat. In case the seed coat does not burst, parts of the embryo force themselves through an opening by the gradual process of elongation (growth by hydration). The hypocotyl is usually the first to elongate and emerge from the seed coat. It grows, bending if necessary, straightway towards the center of the earth, and penetrates the soil. The primary root now continues growth in the soil. In seeds like the Lima bean, the cotyledons and epicotyl are lifted above the soil by the elongation of the hypocotyl, which makes a crook as in Fig. 328, C. In cases like the pea, in which the cotyledons do not leave the seed coat, but remain under ground, the aerial parts are brought through the soil by the elongation of the epicotyl, which may also come up with a crook (A). In the grasses, such as Indian corn, the outermost leaf of the plumule (which

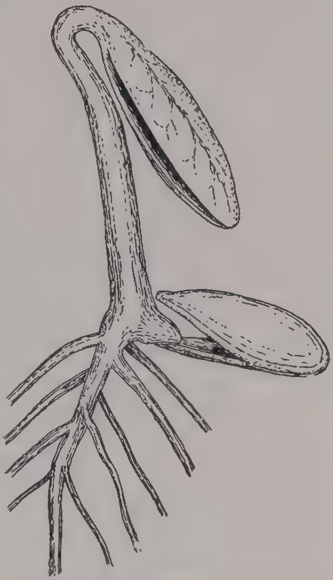

FIG. 329.—Seedling of squash showing the peg or heel holding down the seed coat.

encloses the younger leaves) remains closed and elongates until the surface of the soil is reached when it opens and further growth permits the other blades to unfold (B). In the squash and pumpkin a peg-like out growth of the hypocotyl assists the embryo to free the cotyledons from the seed coat (Fig. 329).

In the meantime digestion and assimilation of stored food continues, and when about all the food primarily stored in the seed is consumed and the seedling plant is able to shift for itself, germination may be said to be completed.

In many seeds between the time of maturity and germination certain internal chemical and histological changes take place which constitute the process of after ripening.

The Development of the Pollen from the Pollen Mother Cells.—In all groups of plants from the Bryophyta to Spermatophyta it has been pointed out that the reduction in the number of chromosomes to one-half takes place in the first mitosis in the spore mother cell. As a result of the reducing division, the spores and the gametophytes developed from them possess the haploid number of chromosomes. Probably in no other cells in the plant kingdom may the reducing nuclear division be so clearly and definitely followed in all details as in the pollen mother cells of certain species of Lilium. The following description pertains especially to *Lilium candidum* and *Lilium martagon.*

The Heterotypic Mitosis or Reducing Division.—After the somatic or equational nuclear divisions have been completed in the sporogenous tissue of the anther, the pollen mother cells, which are polyhedral in shape, make up a compact tissue without intercellular spaces. The cell walls are thin, the cytoplasm dense and rather uniform in structure and the nuclei are relatively large.

The Resting Stage.—In the nucleus the numerous small and irregular chromatin granules varying in size

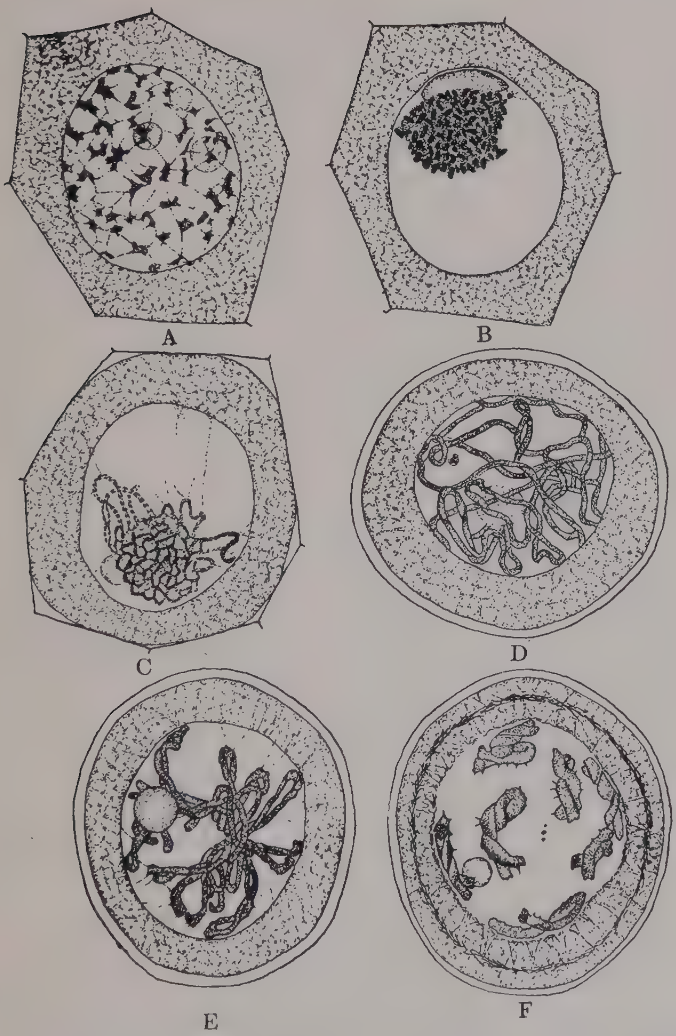

Fig. 330.—Development of the pollen from the pollen mother cell in Lilium. A, the nucleus is in the resting stage; B, the first contraction; C, loosening up of the contracted mass. D, the hollow spirem; E, second contraction, loops radiating from a central tangle; F, cross segmentation of spirem completed and bivalent chromosomes have been formed.

are held upon a delicate linin network. The linin threads are seen connecting the chromatin granules or masses. One to several nucleoli may be present (Fig. 330, A). When the chromatin is in the finely divided state as just stated, the nucleus is said to be in the resting stage.

The beginning of mitosis is indicated by an increase in size of the cell and of the nucleus.

The First Contraction.—The next conspicuous change that takes place is seen in the contraction, or balling up, of the nuclear contents into a dense mass at one side of the nuclear cavity (B). The nucleolus is usually included in the contracted mass. This stage persists for some time, during which the nucleus has increased further in size, and the cell content tends to round off at the corners.

The Formation of the Spirem.—Following the period of the first contraction, the contracted mass begins to loosen and spread out in the nuclear cavity, when it is seen that a continuous chromatin thread, spirem, has been formed (C). The loops and turns of the thread or spirem spread farther and farther apart, and soon become somewhat evenly distributed in the nuclear cavity (D). A very careful study reveals the fact that this thread is composed of chromatin discs or very small masses known as *chromomeres* (C). The chromomeres are held together in the linin thread. Under the most favorable circumstances the chromomeres are seen to be divided lengthwise, and this phenomenon is interpreted as the beginning of a longitudinal fission of the spirem.

With further growth, the spirem becomes thicker and more uniform in appearance, and the individual chromomeres are no longer recognizable. At this stage the longitudinal split can also be seen at least in places, but as the spirem continues to thicken its double nature may be completely concealed, and we have what is now called the hollow spirem (D). The spirem is continuous and without free ends in the species here in question. As the diploid number of chromosomes in Lilium is twenty four, the spirem represents twenty-four chromosomes placed end to end.

In the meantime the cell has completely rounded off, and has built about itself a new cell wall, which is thick and soft.

The Second Contraction.—During the next stage the spirem becomes rearranged in part by which a tangle or knot is formed near the center of the nucleus. From this tangle other portions of the spirem may radiate as loops. This is the second contraction (E).

The Cross Segmentation of the Spirem and the Formation of the Bivalent Chromosomes.—Immediately following the second contraction, the spirem begins to segment transversely into the chromosomes, and these chromosomes approximate side by side to form pairs. Each pair is a *bivalent chromosome*, consisting of two distinct chromosomes that were arranged end to end in the spirem. There are, therefore, twelve pairs or twelve bivalent chromosomes in Lilium. In the state of the second contraction, some of the loops of the spirem that radiate from the tangled portion represent two chromosomes that tend to remain attached for a longer time at the bend of the loop. In such cases the bivalent is formed by the approximation of the sides of the loop. The bivalents thus formed are likely to resemble a figure eight because of the twisting of the loop.

After cross segmentation and the approximation in pairs to form bivalents, the bivalents move apart and become more regularly spaced within the nuclear cavity (F). In this figure eight of the twelve bivalents are shown.

The bivalents may present different forms, depending upon whether the two members are straight or bent, and upon the manner in which they lie with reference to each other. In most cases the two members of the bivalent lie in close contact side by side but almost always twisted about each other. If the members diverge at one end, a Y-shaped bivalent is seen; if both ends diverge, and X-shaped figure results. A loop or a circle is formed when the two members bend apart at the middle and remain in contact at the ends. Some of the bivalents are bent in the form of a U. Those that are bent and twisted most are those that were formed from the knotted or tangled part of the spirem in the second contraction stage. In every case, no matter what form the bivalent may present, each consists always of two rod-shaped chromosomes that have paired in some such manner as described. All the steps in mitosis from the resting stage to the spindle are known as the prophases.

The Spindle Stage, Metaphase.—As soon as segmentation is completed, the formation of the spindle begins. The spindle fibers originate wholly in the cytoplasm. They are arranged radially from the nucleus, or they may form a weft parallel with the nuclear membrane midway between the nucleus and the periphery of the cell (Fig. 330, F). Sometimes both orientations of the fibers occur.

The nuclear membrane now fades away, and the spindle fibers enter the nuclear cavity forming a spindle complex with the bivalent chromosomes included within it (Fig. 331, G).

Certain of the fibers attach themselves to the chromosomes. The fibers of the spindle complex converge at several points to form poles, when the whole figure is designated as a *multi-polar spindle* (G, H). The multipolar spindle is soon transformed into the regular and symmetrical bipolar spindle in which the twelve bivalents are arranged with considerable regularity upon the equator (I). Sometimes the bivalents are arranged like

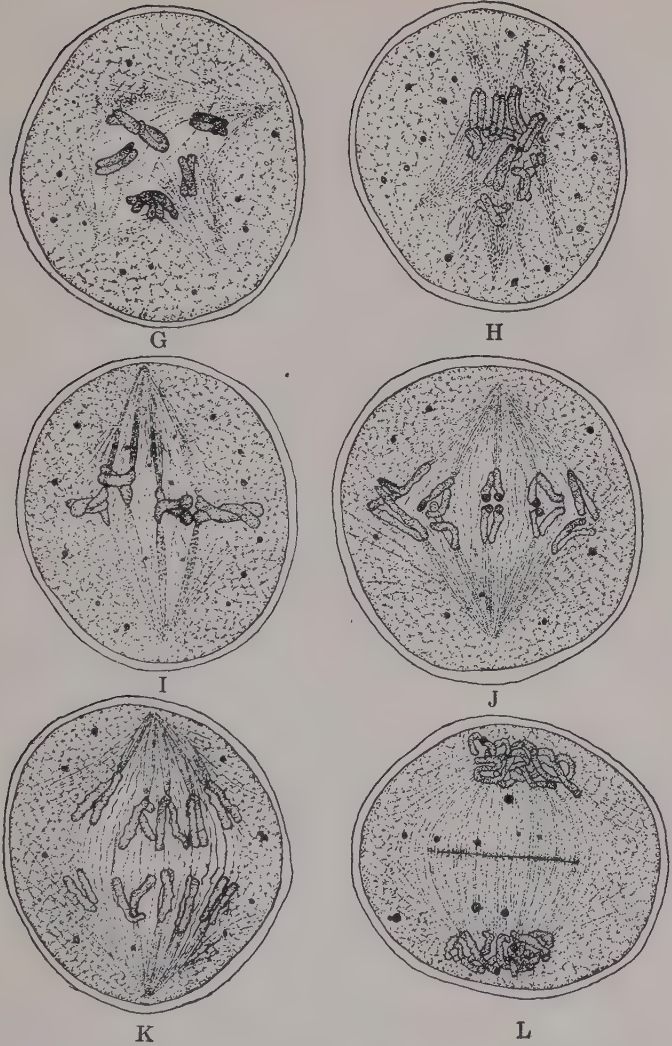

Fig. 331.—Development of pollen in Lilium continued. G, H, the multipolar spindle; I, mature spindle; J, members of the bivalent chromosomes separating, each member has split lengthwise, and the two halves diverge at their equatorial ends. K, anaphase; L, telophase, the chromatin is forming the daughter nuclei.

the spokes of a wheel, but as a rule the arrangement is less regular. Fig. 331, I, represents a spindle in which four bivalent chromosomes are shown. From each member of a bivalent a sheaf of fibers extends to the pole to which it will go. The fibers are attached either to the ends of the chromosomes or some distance from the end at the place of bending in case the members are bent or when they form a ring, a loop, or a figure eight. Certain fibers extend from pole to pole without touching the chromosomes, while others diverge from the poles towards the periphery of the cell.

During the development of the spindle the nucleolus becomes broken up and very small nucleoli are scattered in the cytoplasm.

The Passage of the Members of the Bivalents to Their Respective Poles, or the Anaphases.—The two members of each bivalent now separate, one member going to one pole and the other member to the other (J, K). Each of the two daughter nuclei resulting will consequently possess twelve chromosomes, the reduced number, or just one-half as many as were present in the mother cell.

On their way to the poles the members of the bivalents undergo a change such as takes place in no other nuclear division. As the members separate and sometimes before they separate, in metakinesis, each is seen to be split longitudinally (J). This is the longitudinal fission that was seen in the spirem of the prophase. This fission is a preparation for the second mitosis, i.e., the one that is soon to follow. The two segments resulting from the longitudinal fission pass to the pole side by side, the ends nearest the pole being attached to the sheaf of fibers, while the two ends nearest the equator may diverge to produce the V-shaped figure. If the two members of the bivalent were not attached to the spindle fibers at the ends, but at some distance from the ends, as in the ring-shaped bivalent or that like a figure eight, then the two segments resulting from the longitudinal split would present the form of two U's in contact side by side.

The Construction of the Daughter Nuclei, the Teleophases.—When the chromosomes reach the poles they are, as a rule, closely crowded or massed. The mass soon becomes less compact however. The cytoplasm now seems to withdraw from the mass of chromosomes leaving a colorless cavity at whose periphery a nuclear membrane is formed. The spindle fibers now connecting the two daughter nuclei are *connecting fibers.*

The behavior of the chromatin during the construction of the daughter nuclei, depends upon the lapse of time between the first and second mitoses.

If the second division follows the first immediately, as happens in Lilium during warm weather, the chromosomes on arriving at the poles will all join end to end to form a spirem at once, and the second division will begin without an intervening resting stage (L, M). But, if some time intervenes between the two mitoses, the chromosomes will fragment or reticulate into smaller pieces, so that all identity of the former segments is lost. This reticulation may even proceed to the extent of forming a resting stage. A nucleolus appears in each daughter nucleus, usually closely associated with the chromatin.

As soon as the daughter nuclei are formed, a *cell plate* is developed across the cell at the equator, dividing the pollen mother cell into two daughter cells (L, M). The cell plate is a plasma membrane, formed by the connecting fibers. This plasma membrane splits into two to provide plasma membranes for the contiguous surfaces of the two daughter cells.

The Second or Homeotypic Mitosis.—The second mitosis, i.e., that of the two daughter nuclei, differs from the first, or heterotypic mitosis, in that there is no first nor second contraction stage. The two segments of each chromosome which appear in the equator of the second mitosis were produced by the longitudinal fission which took place during the first mitosis. They do not constitute a bivalent, for as has been pointed out, the two members of a bivalent are not the result of a longitudinal fission but of the approximation of two chromosomes. The second mitosis is therefore an *equational* and not a reducing division.

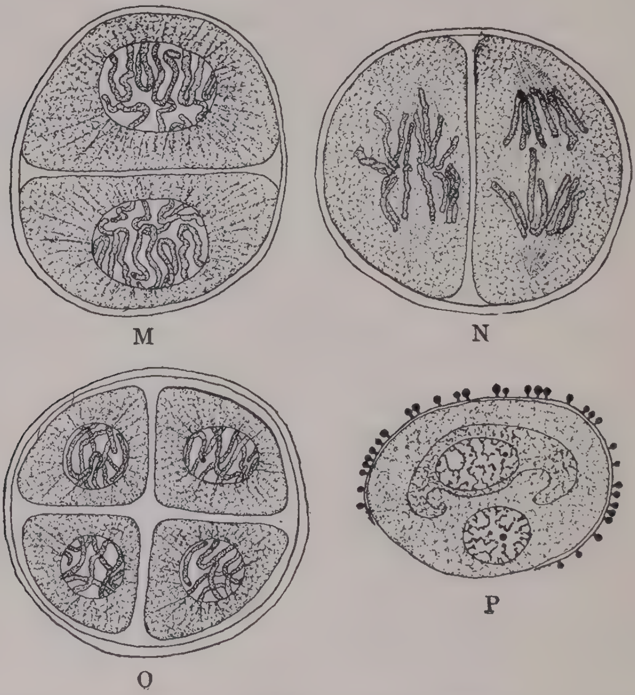

Fig. 332.—Development of pollen in Lilium completed. M, daughter cells resulting from the first division; N, a step in the second division; O, tetrad of four pollen spores; P, mature pollen spore; the crescentic antheridial cell lies free inside the tube cell.)

The second mitosis proceeds as follows. If the chromatin of the daughter nuclei passed into the finely divided state of the resting stage, or became broken into coarser fragments, the spirem is formed from the fragments or from the finely divided chromatin.

If the chromatin segments do not fragment in the daughter nuclei, the spirem is formed directly by the end to end union of those segments.

The spindle is formed as in the first mitosis, i.e., from a multipolar complex of fibers derived from the cytoplasm.

The spirem segments crosswise presumably into the identical segments that came to the daughter nucleus. These segments are arranged upon the spindle in pairs, being attached end to end or side by side (Fig. 332, N). The two members of each pair are supposed to have been derived from one and the same chromosome by the longitudinal division observed in the preceding anaphases. There is no means of knowing, however, that this is so.

In the equator the segments are usually massed together or much entangled. They may radiate from the spindle or lie tangentially upon it (N, left).

With the beginning of the anaphases, the segments, grand daughter chromosomes, separate and pass to the poles (N, right). The granddaughter nuclei are organized, and cell division takes place as in the first mitosis (O).

Maturing of the Pollen.—We now have a tetrad of four pollen spores, each of which matures into a pollen grain of two cells. By the dissolution of the wall of the mother cell the spores are set free in the cavity of the anther, and each rounds out, becoming globular or elongated. A wall of two layers is developed, the exine and the intine. The spore divides in such a manner that one of the cells is crescentic in shape and lies inside the other (P). This crescentic cell, the *antheridial* cell (generative cell) is provided only with a plasma membrane. The cell provided with the double wall of intine and exine is called the tube cell as pointed out in a preceding paragraph.

Kinds of Flowers: Staminate and Pistillate Flowers.—According to our definition, namely, that a flower consists of one or more spore-bearing members with or without accessory parts, a single stamen or a single pistil may constitute a flower. Those flowers, therefore, that consist only of one or more functional stamens are *staminate flowers*, while those consisting only of one or more functional pistils are *pistillate flowers*. These are the simplest flowers. They may be subtended by a bract or surrounded by a collection of bracts, the *involucre*.

The jack-in-the-pulpit or Indian turnip, (Arisaema triphyllum) possesses one of the simplest types of flowers. Here one or two stamens constitute a staminate flower and one pistil, a pistillate flower.

Staminate and pistillate flowers occur in such trees as walnut, hickory, oak, beech and birch.

Staminate and pistillate flowers may, however, possess a calyx or corolla, or both sets of floral envelopes.

In some plants the staminate flowers contain a rudimentary pistil, and the pistillate flowers rudimentary stamens. Such conditions have been brought about by the abortion of one or the other set of spore-bearing members.

Perfect and Complete Flowers.—One of the first principal advances in the evolution of the flower was probably the combination of both stamens and pistils into one flower. Such flowers are termed in descriptive botany *perfect* flowers. If in addition a calyx and corolla are present the flower is known as a *complete flower*. The flower of the tulip, peony and rose are examples of complete flowers.

The Union of Different Parts or Cycles of the Flower.—In the simpler types of flowers the different parts are all free, and borne separately upon the receptacle as in the peony, butter cup, etc. The number of parts may be large,—many stamens sepals and petals. The pistils in such flowers are usually simple, i.e., composed of one carpel. With the evolution toward the higher types of flowers there are seen two marked tendencies, namely, the union of the members of each cycle or set of parts and later the union or adnation of the several sets into one. Accompanying this union there is also a reduction in the number of members of each set or cycle. The union of the members of each set did not take place simultaneously in all flowers. In the tulip the three carpels, for example, are united from an early stage into a compound pistil, while stamens and the parts of the perianth are all separate. Very frequently a greater degree of union is seen in one set than in the other. The petals for example may be united into one piece, while in the same flower the members of another cycle may be separate, or two sets of parts such as corolla and stamens may be united into one piece but separate from calyx or pistil as in the hollyhock. These conditions may be illustrated in the following kinds of flowers:

The Perigynous Flower.—In the flower of the wild rose the sepals form a cup upon whose rim or margin are borne the petals and stamens, the pistil being separate. Such a flower is *perigynous.*

An Epigynous Flower.—If the union proceeds further so that the calyx tube has grown together with the ovary, as in the mock orange (Philadelphus) or carot (Daucus) the flower is *epigynous.*

The Flower of the Compositae.—The highest degree of evolution is regarded as having been attained in the Compositae as represented by the sunflower and dandelion. Here the greatest degree of union has taken place. All parts are united from an early stage in development. The calyx is adnate to the ovary, and when visible is termed the pappus. The five petals are united into one piece, and inserted upon it are the five stamens, whose anthers are united into a tube around the style.

A similar degree of development among monocotyledonous plant is found in the orchids, which represent the highest stage of evolution in that class of Angiosperms.

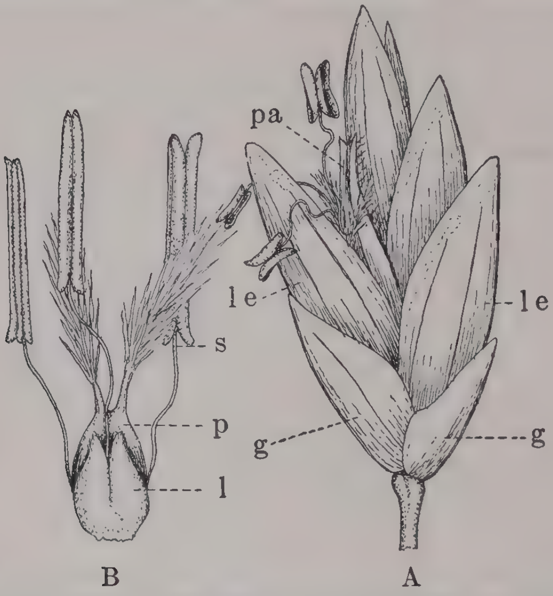

FIG. 333.—A, spikelet and B, flower of a common grass, *Poa annua* L. *g*, glumes; *le*, lemma; *pa*, palea; *s*, stamen; *p*, pistil with two feathery stigmas; *l*, lodicule.

The Flower of a Grass.—Because of the importance of the cereals and forage grasses, the flower of a grass will be of interest. The evolution of the grass flower has proceeded along a line which is distinctly characteristic of this very large order of seed plants.

Fig. 333 illustrates a flower of a common grass. It consists of a pistil (*p*) with two feathery stigmas and three stamens (*s*). Near the base of the pistil is the lodicule (*l*). Calyx and corolla are absent. Each flower is enclosed by two bracts, the *lemma* (*i*) and the *palea* (*pa*), the lemma being below and the palea above. The lemma encloses the palea.

The flowers of grasses are borne usually in *spikelets* (Fig. 333, A).

Grasses are often monoecious or dioecious. Indian corn is typically monoecious, the staminate flowers making up the tassel, the pistillate flowers the ear. Each long "silk" of the ear of corn is a stigma leading to the tip of the ovary which matures as a grain of corn, *caryopsis*.

Arrangement of Flowers, Inflorescence.—The manner in which flowers are arranged upon the primary axis is spoken of as the *inflorescence*. In a broad sense there are two types of inflorescences, the *racemose*, in which the terminal or central flowers are the younger, the older flowers being at the base of the axis, and the *cymose*, in which the terminal or central flower is the oldest. In a racemose inflorescence the succession of development is centripetal, while that in the cymose inflorescence is centrifugal.

Kinds of Racemose Inflorescences. *Spike.*—In the spike the axis (rhachis) is slender, and the flowers are sessile, i.e., with a very short or scarcely perceptible pedicel. Common plantain is an example. The spike in the grasses is called a spikelet, and all that portion above two empty glumes constitutes a grass spikelet.

Spadix.—In the spadix the flowers are sessile, and the axis is generally thick and fleshy. An example is seen in the Jack-in-the-pulpit. The leaf-like structure which subtends or surrounds the spadix is the *spathe*.

Head or Capitulum.—In the head the sessile flowers densely cover the receptacle, which may be conical, flattened or even hollowed out.

Raceme.—In the raceme the flowers are all definitely stalked, and may be subtended by bracts. A typical raceme is found in the Lily-of-the-valley, Berberis and Shepherd's purse.

Corymb.—In the corymb the flowers are arranged as in a raceme, but the pedicels of the lower flowers are longer than the upper, so that all the flowers are borne at approximately the same level, a flat-topped cluster resulting as in the Hawthorne. A corymb is merely a flat-topped raceme.

Umbel.—In the simple umbel the flowers are all stalked in a rosette and spring from a much shortened rhachis. The flower stalks are arranged somewhat like the braces of an umbrella as in the wild carrot.

Panicle.—A panicle arises when the lateral branches of the primary axis, or branches of the first order, also branch, producing branches of the second and higher orders. There are various forms of complicated panicles, such as those composed of small spikes, as in some species of Spraea, in the heads of wheat, rye, oats, etc.

Cymose Inflorescences.—As stated in the preceding, the primary axis terminates in the first and oldest flower. The primary axis or rhachis branches immediately beneath the first flower in such a manner that each lateral axis terminates in a flower after producing one or more lateral axes, which also terminate in flowers and continue the system in a similar manner. The inflorescence of the common wild rose is an illustration of a cyme. In the tulip for example we have a cyme bearing one flower. There are variously complicated forms of cymose inflorescences.

POLLINATION

As regards the phenomenon of pollination in the great classes of seed plants two outstanding differences may be noted, one pertaining to the specific place in which the pollen is deposited, and the other to the manifold character of the agencies involved. In the Gymnosperms pollination consists in the transferral of pollen from the sporangium to the micropyle of the ovule, or in a few cases to the surface of the carpel, near the ovule, and the agencies involved are chiefly wind and gravity. In the Angiosperms pollination consists in the transferral of pollen from anther to stigma, while the agencies concerned are numerous and of the most varied character. With each of the manifold agencies in Angiosperms there is usually some accompanying adjustment and adaptation between the flower and the pollinizing agency.

Self Pollination.—When the pollen of a flower is deposited upon the stigma of the same flower or upon the stigma of another flower of the same plant, self-pollination is effected. In Maize or Indian corn, for example, self-pollination is accomplished when the pollen produced in the flowers of the tassel falls upon the silks (stigmas) of the young ear of the same plant. In many plants the anthers of the flower are in such a position that, on opening, the pollen will be applied to the stigma. This may occur either before or after the flower opens. Certain flowers in various plants do not open at all, and self-pollination necessarily takes place. Such flowers are termed *cleistogamous*. In these only a small quantity of pollen is developed. Certain plants like the common blue violet bear two sorts of flowers, those which open and are showy, and subject to cross pollination, and others that are small and inconspicuous being borne near the ground, the cleistogamous flowers.

Cross Pollination.—It follows from what has been stated in the preceding paragraph that cross pollination is accomplished when the pollen of one plant is deposited upon the stigma of a flower of another plant.

In nature self-pollination is prevented by various means, such as dioecism and the maturing of stamens and stigmas at different times. Or it may happen that the position of anthers and stigmas may be such as to prevent self-pollination. If the anthers mature before the stigmas, the flowers are said to be *protandrous;* if stigmas mature before the anthers, *protogyny* results. Both conditions are efficient in preventing self-pollination. The dwarf larkspur (*Delphinium tricorne*) and the garden Nasturtium (Tropaeolum) are illustrations of protandry, while in the common plantain we have a good illustration of protogyny.

Agencies of Cross Pollination.—The agencies of cross pollination in nature are water, wind, and animals, chiefly insects. In each of these agencies there is invariably some special adaptation between the plant and the pollinizing agency.

Water.—In certain aquatic plants (Naias, Vallisneria, Elodea, etc.) the pollen is set free and borne about in the water or upon its surface. In Vallisneria the pistillate flowers open at the surface of the water where the stigmas are exposed. The minute staminate flowers break away, come to the surface and open, when the pollen is wafted about and by chance comes in contact with the stigmas; or the staminate flower with the open anthers may lodge against the stigma.

Wind.—The wind is doubtless one of the most primitive and the most effective agencies in accomplishing pollination through long distances. Notable instances are found in such forest trees as the pines, oaks, hickories, walnuts. In wind pollinized plants the two outstanding features are the dry and light character of the pollen and the abundance in which it is produced. Many forest trees are dioecious, and, although staminate and pistillate individuals may be far removed from each other, yet owing to the abundance of dry pollen which is carried in all directions, pollination in the isolated tree is likely to be effected.

Insects and Other Animals.—It is in the pollination by insects that the most manifold and marvelous adaptations or adjustments between the flower and its pollinizing agency are encountered. Insects visit flowers to secure food in the form of pollen and nectar, to deposit their eggs, for shelter or for reasons unknown. The pollen of flowers pollinized by insects may be dry and powdery or sticky, or it may adhere in masses, provided with sticky discs, as in orchids, or with a clip-like device by which the masses adhere to certain parts of the insect's body, as in the common milkweed.

In order that the visit of an insect may result in successful cross pollination, that portion of its body to which the pollen adheres when a visit is made must be brought into contact with the stigma of another visited flower. In general the position of anthers and stigmas are such that the insect in taking its food will become dusted with the pollen or apply the dusted portion of its body to the stigma with almost unerring certainty.

Insects visit flowers and accomplish pollination, in certain plants, and the objects of such visits are unknown at present. A notable case in our flora is the Jack-in-the-pulpit and the dragon flower (*Arisaema dracontium*). Small dipterous insects enter the spathes of the staminate flowers, become dusted and are able to escape. When such insects enter a spathe with pistillate flowers, escape may be and often is, impossible, owing to the fact that the animal is held fast between the pistils and the close fitting spathe, where it eventually dies.

The fig wasp (Blastophaga) a very small gnat-like insect breeds in certain figs, that produce staminate and pistillate flowers. When the insect matures it emerges from the ovary in which it was developed, and escapes through the small opening at the end of the fig. On its way out the wasp becomes dusted with pollen. Having thus escaped she enters another and younger fig to deposit eggs, and in so doing carries pollen upon her body, some of which comes in contact with the stigmas of the pistillate flowers.

The figs in which this insect is nurtured are called caprifigs, or wild figs. The fruit of the tame fig tree from which the commercial figs are grown is much better if seeds are developed in them. The tame fig is pollinized, however, by pollen from the wild fig, and in order that pollination may be effected, the wild figs from which the insects are soon to escape are hung upon the branches of the tame tree. The insects on escaping under these conditions enter the young tame figs and the pollen adhering to their bodies is dusted upon the stigmas. The wasp does not breed in the tame fig, owing to the fact that it can not deposit its eggs deep enough in the ovary because of the long style. In the wild fig, however, which has a short style, the deposited egg develops normally.

The Fruit.—In a purely botanical sense the fruit is any part of the pistil that persists and matures. The term is often extended to include accessory and other parts such as the axis, receptacle or involucre, especially if those parts become succulent or pulpy. Seeds may or may not be present.

When the wall of the ovary and adhering parts become dry, membraneous or woody, we have what are termed dry fruits. If the ovary and adhering parts become succulent or pulpy, the term fleshy fruit is applied.

The wall of the ovary in the mature fruit becomes the *pericarp*. The pericarp may differentiate into two or three layers.

The outer layer is the *epicarp* (sometimes merely an epidermis), and the inner the endocarp. Between these there may be a third layer, the *mesocarp*. For example, in the peach or plum, there is a thin epicarp, a thick pulpy mesocarp and a stony endocarp.

KINDS OF FRUITS

Indehiscent and Dehiscent Dry Fruits.—In dry indehiscent fruits the pericarp does not open, but, closely envelops the seed until germination. The seed coat is very thin and membranous.

The Achene.—An achene is a one-seeded dry, indehiscent fruit, as in the dandelion, sunflower, aster.

A Caryopsis.—A caryopsis is a kind of achene, such as a grain of Indian corn. Here the pericarp is thin and tough, closely investing the seed but not separable from the seed coat. In the true achene the pericarp is separable from the seed coat.

The Nut.—In the nut the pericarp is thick and stony or woody. An example is that of the hazel nut (*Corylus americana*) and the chestnut (*Castanea dentata*). The husk of the beech nut and the hazel nut and the spiny husk of the chestnut are involucres.

The Samara and Schizocarp.—These are biolocular or purilocular, dry indehiscent fruits. They usually separate into mericarps. In the *schizocarp*, as found in the carrot, parsnip, and other members of the Umbelliferae and in certain members of the geranium family, the mericarps each resemble a nut or achene. In the *samara*, the fruit of the maple, the mericarps are winged.

Dry Dehiscent Fruits.—In dry fruits that open to release the seeds, the pericarp splits in various ways. In such fruits the seeds possess well-developed, hard and tough seed coats. Among the common dry dehiscent fruits are the following:

Follicle.—A follicle consists of a single carpel which opens along the coherent margins or adaxial suture, as in the common milkweed, larkspurs, and peony.

Legume.—The legume consists of a single carpel that opens both along the adaxial suture and along the median abaxial line. It separates into longitudinal halves. Examples are peas, beans, redbud, black locust.

Silique or Silicle.—The silique is typical of the fruit of the mustard family (Cruciferae). It consists of a compound ovary of two carpels, and opens longitudinally by two valves which separate from the partition.

Capsule.—The capsule is often used in a very broad sense. In the narrower use of the word it is developed from a compound ovary (unilocular or plurilocular) and splits longitudinally into two or more valves from the apex downwards. A typical example is seen in the chickweed (Cerastium). If the longitudinal fissures pass through the partitions, the dehiscence is *septicidal;* but if the fissure is in the middle between each pair of partitions the dehiscence is *loculicidal,* as in the tulip and hollyhock. In the common plantain the capsule opens transversely, the top falling off as a lid. The capsule of the poppy, a pore-capsule, opens by pores near the top.

Succulent Fruits.—In this class of fruits, the pericarp or certain of its layers remain pulpy. These fruits may be dehiscent or indehiscent. The succulent indehiscent fruits commonly met with are the drupe, berry, and pome.

The drupe, or stone-fruit, has a thin epicarp, a fleshy mesocarp, and a stony endocarp which encloses a seed with a thin seed coat, as in the plum and peach.

The *pome* consists of a tough epicarp, a pulpy or succulent mesocarp and a leathery or bony endocarp. Examples are apple, pear, haw, etc.

The berry has a more or less firm or tough epicarp, and a pulpy mesocarp in which the seeds are embedded. Examples are, grape, tomato, currant, gooseberry, cucumber. The fruit of the pumpkin and melons is often called a pepo. Allied to the berry are the citrus fruits such as the orange, lemon and grape fruit. Here the pericarp consists of a tough outer layer, commonly called the rind, and a pith-like inner layer. From the innermost layer of the wall of the plurilocular ovary protuberances are developed at an early stage, which fill these cavities or loculi as isolated, and closely packed masses of succulent tissue known as the pulp.

Succulent Dehiscent Fruits.—In this type of fruit the succulent but not pulpy pericarp bursts and discharges the seeds in which the seed coat is usually strongly developed. Examples are the fruit of touch-me-not (Impatiens) and buckeye. The term succulent capsule may be applied to such fruits as the buckeye (Aesculus) and Impatiens. The fruit of the black walnut corresponds to the drupe. The outer succulent layer or hull bursts, and the stony endocarp surrounds the seed which has a very thin seed coat.

Special Kinds of Common Fruits.—The *blackberry*, *raspberry* and *mulberry* are often called aggregate fruits. The raspberry is a collection of drupelets which are easily separable as a cup-shaped mass from the torus or receptacle. In the blackberry the drupelets tend to adhere to the receptacle, when the whole is pulled off.

Strictly speaking, the fruit of the *mulberry* is an achene covered by the succulent berry-like calyx, the whole spike becoming the aggregate fruit.

Strawberry.—The strawberry is often referred to as an accessory fruit. It consists of a greatly developed, pulpy torus in the surface of which are the numerous small achenes. The pineapple is also an example of an aggregate fruit.

The Acorn.—The fruit of the oak (Quercus) is a nut or acorn resting in a "cup." The cup is a kind of involucre consisting of a number of small bracts grown together.

The Hickory Nut.—In the hickory nut and pecan the part which splits open is called the husk or shuck; it is probably a modified involucre. The endocarp is hard and stony; the seed coat is very thin.

The Fig.—The fig consists of a hollow, succulent, pear-shaped axis containing the fruits within. These fruits are achenes.

Seedless Fruits, Parthenocarpy.—Many fruits, as the commercial banana, navel or seedless oranges and many others bear no seeds. The term "blind" fruit is applied to cases in which the pistil develops into the normally appearing fruit but without seeds. Frequently many fruits of the maple (Acer) will thus develop. These phenomena may be referred to as parthenocarpy, or the formation of fruits without seeds. The cause in all cases is not known.

The seedless orange arose doubtless as a bud sport. The origin of many seedless fruits is unknown at present. They probably originated in nature and were not "created by a horticultural wizard."

Dispersal of Plants.—Plants are distributed over the surface of the earth by means of spores, seeds, and by the development of adventitious growths from leaf, stem and root, and in the case of lower plants from vegetative parts of the thallus. In many instances vegetative parts become separated by the death and decay of connecting portions, after which the branches continue growth as distinct individuals. Many such cases have been noted in foregoing paragraphs dealing with the several plant organs and with the life-histories in the several groups.

In the scattering of seeds, spores and other plant parts, the most effective agencies of the environment are wind, water, and animals including man. Fruits provided with hooks and spines adhere to the feet and coats of various animals. Many fruits sought by birds and other animals for food have the vital parts of the seeds protected by coverings which resist the digestive action of the alimentary tract, and become distributed far and wide.

As regards the dispersing agencies of wind and water, the numerous adaptations between these agencies and the parts dispersed are so numerous and so easily understood that the enumeration and illustration of typical cases here seem superfluous.

Lastly, self dispersal occurs in many plants of the great groups. Seeds are ejected by the fruits themselves as they mature and dry out, or fall from the plant as the result of some external force. The mechanical action due to changes in moisture temperature, and so forth, range in variety from that of the discharge of spores from sporangia to the shrivelling and opening of a bean pod.

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